Towards an understanding of complexity: How body sizes, preferences and habitat structure constrain predator-prey interactions

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“Stuff your eyes with wonder . . . live as if you'd drop dead in ten seconds. See the world. It's more fantastic than any dream made or paid for in factories.“

Ray Bradbury, Fahrenheit 451

für meine Familie

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1. General Introduction

1.1. Aims and scope

With the concepts, experiments, models and results presented in this thesis I have interwoven knowledge, ideas and approaches from all relevant hierarchical levels in ecology: While optimal foraging models from behavioural ecology focus on mechanisms at the very individual level there is the consumer-resource functional response serving as a bridge to population ecology in its classical sense. Above, the macro-ecological theme of the metabolic theory of ecology with its core element "allometric scaling" provided a general framework beyond detailed species-specific classifications. This gave the possibility to unify all these levels under the umbrella of community ecology by addressing questions about general rules that govern energy flows within natural food webs as well as the structure and stability of these fundamental entities of ecosystems.

1.2. Ecology: interactions and stability

a) The science of interactions or how this thesis unfolds

Before I go into the details of food-web theory and functional responses it seems worthwhile to recapitulate what the subject I have been dealing with is all about:

"Ecology is the scientific study of the interactions that determine the distribution and abundance of organisms" (Krebs 2001).

Although Häckel (1866) primarily introduced the term "ecology" almost 150 years ago, it was not until Krebs' definition (firstly formulated in the early 1970ies) that the central importance of *interactions* has been carved out word by word. Nevertheless, interactions have always been the focus of the scientific endeavours under ecology's roof including abiotic as well as biotic factors but also interactions at intra- and interspecific, or even at population or community levels. Consequently, the intriguing complexity that we find in nature has to be addressed by research aiming to understand the rules and patterns that shape the interaction networks connecting individuals and populations. Regarding our huge knowledge gaps about earth's biodiversity (Mora *et al.* 2011) - even in well-sampled temperate zones (Creer *et al.* 2010) - the exploration of the vast number of possible interactor pairs in nature appears absolutely intractable. This implies that there is an urgent need for an alternative framework to understand individual and population interactions as well as ecosystem processes in a generalised and rather quantitative way as we cannot wait until all species on earth are determined.[1]

Nevertheless, ecologists of the past decades have managed to get new insights by the application of the scientific method comprising description, theory and experiment. Hence, observations and descriptions of patterns should serve as starting points for the formulation of hypotheses with the help of sound theoretical thinking and subsequent testing in experiments. New insights from

1 Obviously, I do not want to bad-mouth traditional taxonomic classification, which is definitely worthwhile and important to understand evolutionary and ecological processes and needs much more support than it gets nowadays (Boero 2010; Bacher 2012). It is rather that most, if not all, problems we are facing today need a diversity of approaches to tackle them and I think that quantitative, continuous data have many considerable advantages over categorical data like species lists.

experiments might then serve to sharpen the profile of the hypotheses and go back to the experimental (and the observational) arena again.

Following this almost-trivial (*sic!*) scientific cooking recipe I built my thesis on the observations of regular patterns in body-size distributions in natural communities [(Elton 1927; Sheldon, Sutcliff, Jr., & Prakash 1972; Peters 1983; Cohen *et al.* 1993; Brose *et al.* 2006a); see chapter 1.5a]. The conceptual framework that then helps to interpret and understand this patterning is fostered by allometric scaling rules [(Kleiber 1932; Peters 1983; Brown *et al.*

Box 1.1.: Glossary

Allometric scaling: Describes the relationships of various biological traits and rates in dependence of an organism's body size. The fundamental principle follows simple geometric arguments, as surface to volume ratios do not increase (or decrease) linearly with changing sizes. Today, most allometric scaling relations are formally defined as power laws (i.e., linear in on log-scale). The most important allometric scaling in terms of population and community ecology is that of the metabolic rate as it is critical for the flow and dynamics of the fundamental biological currency: energy (see chapter1.5 and Box 1.3.).

Consumer: Following a broad definition, any heterotroph organism. Consumers can be classified into functional groups (see Box 1.2.). This thesis focusses on *true predators*.

Food web: The description of who eats whom in an ecological community.

Functional response: The feeding rate of a consumer (i.e., predator) described as a function of the density of the resource (i.e., prey). The two fundamental parameters are the capture rate (alternatively: attack rate) and the handling time.

Interaction strength: Generally, the net effect of one species on another species within a community. In the majority of cases, this implies direct trophic effects. Theory predicts that linear interaction-strengths cause highly unstable food webs and empirical evidence suggests that they usually are non-linear. Functional responses are widely-accepted as a way to describe non-linear interaction strength and to implement them in food web models. See Berlow et al (2004) for a detailed review on the topic.

Metabolic rate: The amount of energy expended by an organism in a given time.

Resource: Any organism that gets (partly or entirely) consumed by the consumer. The empirical data in this thesis includes resources that are herbivores, detritivores and omnivores that were usually consumed entirely by their true predators.

Trophic Level (T_L): The position of an organism (or a functional group) in the food chain (or food web) as pictured by the classical *pyramid of numbers* (Elton 1927). There primary producers (e.g., vascular plants) are at the bottom with $T_L = 0$, primary consumers (e.g., herbivores) have $T_L = 1$ and the levels of higher order consumers (e.g., predators) $T_L \geq 2$. Accordingly, trophic level is calculated by "one plus the average trophic level of the prey". For alternative definitions see Williams and Martinez (2004a).

2004); 1.5a] and theoretical population biology [(May 1974; Yodzis & Innes 1992); 1.6a]. Subsequently, I tested my hypotheses in experiments that are based on the long-standing fields of optimal foraging theory [(MacArthur & Pianka 1966; Pyke, Pulliam, & Charnov 1977; Stephens & Krebs 1986); 1.4] and predator-prey functional responses [(Holling 1959a; Murdoch & Oaten 1975); 1.6a,b]. In conclusion, I propose interaction models that are easy to retrace with a limited set of parameters involved (related to body size and habitat structure) and that fit well with empirical observations.

b) Complex food webs as conceptional pictures of ecological communities

Although this thesis does not focus on food webs in any specific context there are some basic principles about this branch of community ecology that I think are vital for the reader to understand the following chapters. Foremost, a food web can be roughly described as the species inventory (i.e., the entirety of populations) of a given habitat (i.e., ecosystem) plus the trophic links that connect all the species within the web. The trophic links then constitute the channels where energy and nutrients circulate through the ecosystem with its biotic (and, sometimes included, abiotic) compartments. Therefore food webs have been described as "road maps through Darwin's famous entangled bank" (Pimm, Lawton, & Cohen 1991) but, to follow this analogy, large scale maps are rare. Often, species are lumped into functional groups (e.g., "unicellular algae" or "decomposers") or trophic levels (in the most extreme case the complex food web is conceptually simplified to form a food chain). Fortunately, though, the number of highly resolved webs is increasing [e.g., for a sample of current high-qualitative datasets see (Riede *et al.* 2011)]. The majority of the empirical food webs is qualitative rather than quantitative, i.e., the feeding links between species are described in a binary way as present or absent. One reason for this shortcoming is that direct observation of feeding is intractable in many cases (e.g., for very small organisms). Beyond that, methods for indirect observation are being developed and increase in application but their capability to provide high-resolution at taxonomy levels is limited [e.g., for stable isotope data (Vander Zanden & Rasmussen 2001; Post 2002)]. Beyond details of methodological potential, full quantitative sampling of entire complex food webs would imply enormous logistical, expensive and time-consuming efforts and therefore other methods for the determination of the quantity of the interactions (i.e., the interaction strength) have to be considered. The term "interaction strength" in

this context is central for the understanding of the following chapters and therefore the reader should keep it in mind.

c) What is stability in ecosystems and how does it originate?

Today, stability is one of the most important concerns of ecological research as ecosystems are increasingly stressed due to human interventions such as eutrophication or habitat fragmentation. One critical question that arises is whether we can preserve ecosystem services that are vital for, e.g., agricultural productivity in spite of these anthropogenic stressors. Therefore the answers to the question "what makes ecosystems stable" are of central importance for the future of mankind. To define stability, there are several formal criteria [e.g., resilience or variability, see (Pimm 1984)] but as a general and informal version one could translate the enigma of ecological stability into the simple question "why are there so many species on earth and how can each of them persist for thousands of generations?".[2] This question has puzzled ecologists for decades resulting in some of the most influential papers in ecology and has become renowned as the diversity-stability debate (May 1972; McCann 2000). The gist of the debate is the question if large, complex systems will be inherently stable or not. Before May's seminal work (1972), ecologist's believed complex systems such as ecological communities were more stable if they were larger (MacArthur 1955; Elton 1958). Observational evidence suggested that small and simple communities were prone to the most pronounced population fluctuations (hence, with the highest risk of extinctions). Later Gardner and Ashby (1970) showed numerically that not only the sheer size of a web (i.e., the number of nodes corresponding to species in a food web) but also the connectance (i.e., the total number of links within the web) is critical for stability with the result that a high degree of connectance increases the probability for instability. Two years later Robert May (1972) came out with his ground breaking paper that proved analytically that large complex systems with random connectance and average interaction strengths tend to be highly unstable. At the end of the paper his speculations about varying interaction strength and a certain patterning of link-distribution in food webs as possible reasons for the stability observed in nature then paved the way for food-web research in the following decades. There are many papers worth mentioning [see recent reviews about ecological networks

2 Thinking of evolutionary or geological time-scales, two issues arise: (1) sooner or later every single species will become extinct and, (2), as species are no fixed entities but are somehow arbitrary, human-invented units within an evolutionary continuum, the problem becomes almost impossible to grasp. Besides these rather philosophical problems, I will focus on ecological time-scales for the remainder of the thesis.

(Ings *et al.* 2009), food web models (Petchey *et al.* 2011) or interaction strength in food webs (Berlow *et al.* 2004)], but for the reasoning in this thesis I just want to name a few of the studies that corroborated May's early speculations. Firstly, the distribution of interaction strength has been shown to be far from uniform and particularly the importance of weak links in food webs has been highlighted in a number of studies [e.g., (McCann, Hastings, & Huxel 1998; Berlow 1999; Neutel, Heesterbeek, & de Ruiter 2002)]. Furthermore, the non-random distribution of feeding links associated with regular size distributions has been shown to be crucial for stability [e.g., (Emmerson & Raffaelli 2004; Brose, Williams, & Martinez 2006b; Otto, Rall, & Brose 2007; Berlow *et al.* 2009; Riede *et al.* 2011)].

So much for the introductory framework for the following chapters. At this point I will leave the community level of the ecological hierarchy and focus on the interactor pair that forms the basic unit of any food web.

1.3. Predators and prey

Though we know that there are a plethora of different forms of inter-individual-interactions in nature (e.g., direct effects like plant-pollinator mutualism or indirect effects such as recruitment facilitation in plants or sessile animals), the most important form in energetic terms are direct trophic interactions. These feeding interactions might be distinguished regarding the classification of what kind of organism gets consumed (e.g., herbivore or bacterivore interaction) or rather by a functional characterisation (see Box 1.2).

Box 1.2.: Functional groups of consumers

During their lifetime, many consumers may belong to more than one of the following functional groups. Furthermore, this kind of categorisation is always arbitrary and some of the categories are not mutually exclusive nor is this list exhaustive.

Grazer: Grazers consume organisms that grow in colonies or lawns. In most cases the resources are autotrophs (plants, algae) but there are also grazers consuming heterotrophs like fungi, bacteria or animals (e.g., Bryozoa). Normally, grazers feed on a large number of resource individuals during their lifetime. Striking examples are large herbivorous mammals like moose or wildebeest but also some caddisfly larvae or sea urchins. In pelagic systems, filter feeders like baleen whales correspond to terrestrial or benthic grazers. Most grazers are larger than their resource. (Some definitions include that grazers do not kill their (modular) resource organisms, but this holds only for a subset of animals that are denoted grazers).

Parasite: Parasites consume only parts of their resource (i.e., host) and only occasionally kill their host. Most parasites attack only one or a few hosts during their lifetime. Parasites are usually smaller than their resource.

Parasitoid: A parasitoid might be called an intermediate form of a parasite and a predator. The parasitoid larva kills the host and completely consumes it. A parasitoid usually consumes only a limited number of resource individuals during its lifetime (often only one). Parasitoids exist exclusively within the holometabolous insect groups of Hymenoptera and Diptera. They are roughly the same size as their host (slightly smaller than host according to Brose et al 2006a)

True predator: True predators pursue and kill their prey and often consume the whole organism. They attack a (large) number of prey individuals during their lifetime. Examples are falcons, sharks or dragonfly larvae but also phytoplankton feeders like copepods or seed-predators like rodents or ants. To overcome prey individuals, predators are usually larger than their prey. Exceptions from this rule exist and might be found among group hunters (e.g., wolves; social insects), or animals employing pitfall trapping like web-building spiders or ant-lions. As many grazers are predators in this sense, a vague line of demarcation between predators and whole-organism consuming grazers like snails or baleen whales can be drawn by the approach of attack toward the resource: while predators attack specific individuals the typical grazer or filter feeder attacks the colony or cloud of organisms as a whole.

The focus of my work was set upon *true, generalist* predators, i.e., animals that attack and consume whole organisms alive while the prey might stem from a broad spectrum of different taxa (and body sizes). The investigation particularly of *generalist* predators is worthwhile for several reasons: (1) they can be very important providers of ecosystem services such as pest (Symondson, Sunderland, & Greenstone 2002; Schmidt *et al.* 2003) or human disease vector control (Samish & Rehacek 1999), (2) large and mobile generalist predators may serve as connections between structurally isolated web compartments (Scheu 2001; McCann, Rasmussen, & Umbanhowar 2005) and, in a more general way (3) their meaning for the stability and persistence of food webs has been highlighted by a recent theoretical study (Gross *et al.* 2009).

Two central arguments make predator-prey interactions markedly suited for the conceptual framework addressed in this thesis: First, and in contrast to other forms of trophic interactions (e.g., parasitism), the interaction between a predator and its prey is usually fatal for the victim with the whole biomass transferred to the predator that generally consumes a (high) number of prey items during its lifetime. Second, and deductive from the first argument, the body-sizes of consumers and resources not only shape the interaction in a literal way but at the same time permit an energetically-based modelling of biomass budgets between populations. I will engross my mind into this later in chapter 1.6.. But before, I will look at certain constraints shaping the way predators and prey interact. (For the remainder of this thesis I will stick to the terminology of predators and prey, though many principles that I describe also apply to other groups of consumers).

1.4. Optimal foraging theory

Firstly introduced by MacArthur and Pianka (1966) and Emlen (1966), optimality modelling became an important concept in behavioural and evolutionary ecology during the 1970ies and 1980ies (Werner & Hall 1974; Pyke *et al.* 1977; Mittelbach 1981; Stephens & Krebs 1986). Its core messages comprises that foragers (e.g., predators) generally shall seek to optimise their net energy gain following prior optimisation due to evolutionary constraints. This includes two major conceptual advancements that are vital for the understanding of current food-web theory and particularly the work presented in the following chapters: (1) all organisms rely on the ubiquitous currency of (bio-)energy and, (2), they have evolved to use and gain this currency with high (i.e., optimal) efficiency. Though this includes a couple of simplifications,

ecological thinking has profited tremendously from this concept. Optimality modelling and foraging theory have then been categorised into four subjects (Pyke *et al.* 1977): While the first is dealing with the optimal diet (i.e., which food types or which size classes of prey organisms to choose) the latter three all deal with spatial patterns (optimal patch choice, optimal time allocation per patch and optimal patterns and speed of movement). As spatial patterns have been standardised in the experiments and disregarded in the model approaches that came to application within this thesis I will focus on the optimal diet theory and disregard the other categories here. Some of the most prominent studies within the optimal foraging literature deal with simple, body-size related questions that can be seen as the predecessors of the models that I used in the following chapters [e.g., (Werner & Hall 1974; Elner & Hughes 1978; Mittelbach 1981)]. The basic idea behind this is a hump-shaped relation between the body size of the prey and the net(!) energy gain that the predator can get. In other words: to consume relatively small and relatively large prey is energetically inefficient while there is an optimal prey size where the net energy gain is maximised. Naturally, there are other aspects of optimal diet choice such as stoichiometry (Elser *et al.* 2000; Sterner & Elser 2002). According to this concept consumers need a mixed diet in order to optimise a required composition of key nutrients, which has been documented for generalist herbivores (Westoby 1974; Newman *et al.* 1995) as well as generalist predators (Greenstone 1979; Mayntz *et al.* 2005; Jensen *et al.* 2012). While both these aspects seem worthwhile to investigate, the grand advantage of the prey-size optimality-approach over the optimal-stoichiometry approach is two-fold: First, body sizes are much easier to measure and to manipulate experimentally than nutrient composition. Second, the direct interdependency between body size and energy content of the prey allow for the construction of very simple, allometrically-constrained predator-prey models. Let me introduce the basics of allometric scaling and the macroecological meaning of it in the following chapter.

1.5. The ecological meaning of body size

a) Empirical body size patterns and allometric scaling

The existence of general patterns and regularities of the body-size distributions in natural communities has been captivating ecologists for almost a century (Elton 1927; Brooks & Dodson 1965; Sheldon *et al.* 1972; Cohen *et al.* 1993) and remains doing so (Woodward *et al.* 2005; Brose *et al.* 2006a; Otto *et al.*

Box 1.3.: Allometric scaling laws: Allometric scaling laws are generally described as simple power laws:

$$A = A_0 M^s \quad \text{B1.3.1,}$$

where A is a dependent variable (e.g., flight speed, Alerstam et al 2007), A_0 is a normalization constant, M is body mass and s is the scaling exponent. If $s = 1$, then the scaling is called isometrical. For all other values of s, the scaling would be allometrical. Traditionally, these scaling laws are pictured in the log-log space with linear axes:

$$\log A = \log A_0 + s \log M \quad \text{B1.3.2}$$

where s is the slope of the allometric relationship. Most empirical values of s are reported as multiples of 0.25 according to the metabolic theory of ecology (Brown et al. 2004). Allometric scaling laws provide simple yet widely applicable null models for the analysis of patterns and structures that are object to community and macro-ecology.

2007; Riede *et al.* 2011). Besides these patterns there is another intriguing feature of body size that has been attracting the attention of biologists and physiologists over an even longer period: the phenomenon of allometric scaling (Snell 1892; Kleiber 1932; Peters 1983; West, Brown, & Enquist 1997; Alerstam *et al.* 2007). There the relationship between body size of organisms and diverse biological rates and traits is described with power laws on the base of simple geometric considerations and assumptions [see (Peters 1983; Hendriks 1999) for reviews; also see Box 1.3]. Although there are many scaling relationships that have been studied from bird flight speed (Alerstam *et al.* 2007) to life span (Western 1979), the one allometric scaling law that has drawn by far the most attention for decades and remains hotly debated is specifying the relationship with metabolism (Brown *et al.* 2004; Glazier 2010; Kolokotrones *et al.* 2010; Isaac & Carbone 2010). The reason why the allometric scaling of metabolism has gotten and still gets so much attention, especially from community and macro-ecology, is to be explained by its far-reaching consequences for the existence of food-webs: e.g., if metabolism would be scaling isometrically, the absolute energetic demands of individuals on higher trophic levels would be much higher presumably resulting in totally different structures of ecological communities. Therefore it has been proposed, that the mechanistic principles of the so-called *metabolic theory of ecology* (Brown *et al.* 2004) are vital for community stability due to several, direct and indirect, pathways [e.g. (Brose *et al.* 2006b; Otto *et al.* 2007; Berlow *et al.* 2009)].

This concept of the allometric scaling of metabolism is closely related to mass-abundance relationships that have been described by Elton (1927) as the *pyramid of numbers* that has subsequently been documented repeatedly for population sizes as well as for species diversity (Damuth 1981; Nee *et al.* 1991; Cohen, Jonsson, & Carpenter 2003; Jennings & Mackinson 2003). Though Eltons'

classical concept related the structure of the pyramid to trophic levels rather than body size alone, we now know that both are strongly interdependent (Riede *et al.* 2011). Generally (and specifically for this thesis examining feeding rates of *true predators*), we can conclude that small numbers of large top predators feed on higher numbers of inferior order predators which themselves feed upon decomposers and primary producers with the highest numbers and the smallest body masses. For the sake of clarity, I have to add that there are many exception to this rule (e.g., vascular plants like trees at the bottom of food webs or host-parasite interactions where the parasite is several orders of magnitude smaller than its host) but these relationships are skipped within a large fraction of recent food web studies focussing on allometry (e.g., Brose et al (2006a) state that they focus on predator-prey relations because there was the most comprehensive database for all ecosystem-types).

These underlying principles of the allometry of life have been used to parametrise realistic models of population dynamics [e.g., (Yodzis & Innes 1992; Brose *et al.* 2006b; Weitz & Levin 2006; Rall, Guill, & Brose 2008; Berlow *et al.* 2009; Binzer *et al.* 2011)]. But to understand the principles of these models one has to delve into the historical development of (theoretical) population biology first in chapter 1.6., but before I shortly want to explain the roots and the consequences of the strictly allometric approach applied in chapters 2.2. and 2.3..

b) Size spectra and the "curse of the latin binomial"

Historically, the ecological importance of body size was noticed early on - particularly in Elton's outstanding work (Elton 1927). Nevertheless, during the following decades the body-size relations in ecological communities have been tackled quite differently between terrestrial and aquatic ecology due to "departmental borders" (Raffaelli, Solan, & Webb 2005): While terrestrial ecology has largely denoted body-sizes as a characteristic trait of individual taxa (with mean adult or population body mass) (Cohen *et al.* 1993; Brose *et al.* 2006a), aquatic ecologists and fisheries scientists have used an alternative approach where they treat all organisms as particles to create size classes called spectra (Sheldon *et al.* 1972; Petchey & Belgrano 2010). It has been criticised that the taxonomy-focussing of terrestrial and freshwater ecology might somehow and sometimes be misleading to get vital insights at community levels [Raffaelli's (2007) *curse of the Latin binomial*] and that the taxonomy-neglecting approach from aquatic sciences as a way to see things differently could pave the way for new findings. Only recently, though, the two approaches have started to cross-

stimulate each other by incorporating species information in fisheries models that used to work exclusively with size information (Andersen & Beyer 2006) or by comparative studies of empirical size spectra from soil and aquatic food webs (Reuman *et al.* 2008). However, interactions happen at the individual level but the former studies explored the body size versus taxonomy phenomena on the community level. Therefore, parts of this thesis (Chapter 2.2. and 2.3.) addressed questions on the allometry of interaction strengths according to these approaches. This implicates the striking advantage to build relatively simple models that do not need parametrisation for every single species. For a reasonable application, however, it seemed useful to have (1) a wide range of body sizes of predators and prey (i.e., body-mass ratios), (2) several species that are relatively similar in behaviour and mode of foraging and, (3), the organisms shall come from similar habitats.

All the concepts presented in chapters 2.1. - 2.3. are finally included in the model framework of the functional response that itself relates to realistic dynamic population modelling that I want to introduce in the next chapter.

1.6. Theoretical population ecology

a) Simple mathematical descriptions of population dynamics

The earliest attempts to seize population dynamics mathematically were dealing with the growth of human populations and the arising problems of feeding and sustaining these populations (Malthus 1798; Verhulst 1838). Malthus (1798) propagated (and feared) exponential growth of human populations accompanied by an insufficient linear increase of agricultural production thus resulting in the so called *Malthusian catastrophe*. There the population dynamics with the biomass density N are described with initial population $N_{0,}$ growth factor r and time t:

$$N(t) = N_0 e^{rt} \qquad (1.6.1).$$

This very simple formulation merges diverse biological variables into only one factor. As r can be either negative (i.e., the population will die out for $r < 0$ and $t \rightarrow \infty$), neutral ($r = 0$, the population density remains constant) or positive, it implies that for values $r > 0$ it would predict indefinite growth. In fact, the exponential growth can be shown only initially for laboratory organism like bacteria but is only a vague approximation to biological reality. 40 years later

Verhulst (1838) formulated the *logistic equation* based on Malthus' assumptions:

$$\frac{dN}{dt} = \alpha N\left(1-\frac{N}{K}\right) \qquad (1.6.2),$$

where α is the maximum per-capita rate of change or the intrinsic rate of increase, and K is the carrying capacity (sometimes also referred to as equilibrium density). Note that the logistic growth described by Verhulst's equation yields higher biological plausibility by introducing the possibility of finite growth through the carrying capacity that can be interpreted in different ways (e.g., nutrient or space limitation).

The following remarkable progress was made by Alfred Lotka and Vito Volterra in the 1920ies (Lotka 1925; Volterra 1926). Independently from each other they developed the formulations that later on became known as Lotka-Volterra equations of predator-prey population dynamics. The intriguing feature here is that two differential equations describe the populations of predator and prey, respectively, and they are coupled by the following terms:

$$\frac{dN}{dt} = \alpha N-\beta NP \qquad (1.6.3),$$

and

$$\frac{dP}{dt} = \gamma NP-\delta P \qquad (1.6.4),$$

where N and P are the biomass densities of the prey and the predator, respectively, α and δ are the per-capita rate of change ("growth term" and "death-rate", respectively), while β and γ are the respective rates of change due to the predator-prey interaction. Though in many cases these equations have served as a good approximation and still come to application in many studies, the linear density-dependence and the potentially non-saturating predators have been criticised (Leslie 1958; Holling 1959a; Berryman 1992; Koen-Alonso 2007).

This issue could be solved by the introduction of the functional response framework by Solomon (1949) and Holling (Holling 1959a; b). There the feeding rate F of a predator is described as

$$F = \frac{a N}{1+a h N} \qquad (1.6.5),$$

with the attack rate a and the handling time h. The attack rate has later been called capture rate [as it rather corresponds to the rate of *successful* attacks,

(Koen-Alonso 2007)] and is expressed as a "search velocity" with the unit [m^2/s] or [m^3/s] depending on the ecosystem type.

Traditionally, Eq. (1.6.5) has been classified as type II functional responses where the constant capture rate causes a hyperbolic curve. In contrast, the sigmoid type-III response includes a capture rate that varies with prey density $a = bN^q$, where b is a search coefficient (hereafter: capture coefficient) and q is a factor converting hyperbolic into sigmoid curves (hereafter: capture exponent):

$$F = \frac{b N^{1+q}}{1+b h N^{1+q}} \qquad (1.6.6),$$

Accordingly, the traditional classification defines the type-II response with $q = 0$ and the type-III responses with $q = 1$ (Real 1977) while the meaning of values for $0 < q < 1$ (denoted as intermediate or modified type-II response) have largely been ignored for a long time. Only recently, this meaning has been examined in two theoretical studies (Williams & Martinez 2004b; Rall *et al.* 2008), but I will come back to these studies below.

As Eqns. (1.6.5) and (1.6.7) are suitable for simplified predator-prey relations it has been extended to a multi-species version (Murdoch & Oaten 1975; Koen-Alonso 2007):

$$F_{ij} = \frac{b_{ij} N_j^{1+q}}{1+b_{ij} h_{ij} N_j^{1+q} \sum_{k=1}^{k=n} b_{ik} h_{ik} N_k^{1+q}} \qquad (1.6.7),$$

where the density-dependent feeding rate F_{ij} of predator i on prey j is characterised with the specific parameters b_{ij}, h_{ij} and q_{ij} but also on the densities and prey-specific functional response parameters for all other prey $k = n$ the predator feeds on (Koen-Alonso 2007).

The previous formulations represent mechanistic versions of the functional response. In contrast, the basic form (Eq. 1.6.5) has been formulated according to a more phenomenological approach (Real 1977, 1979) where maximum ingestion rates F_{max} and half-saturation densities N_0 are defined by capture rates and handling times as follows:

$$F_{max} = \frac{1}{h} \qquad (1.6.8),$$

and

$$N_0 = \frac{1}{a\,h} \qquad (1.6.9).$$

The deductive formulation of the functional response is used in many theoretical studies on population dynamics and food web stability [e.g., (Yodzis & Innes 1992; McCann & Yodzis 1994; McCann *et al.* 1998; Williams & Martinez 2004b; Brose, Berlow, & Martinez 2005; Brose *et al.* 2006b; Rall *et al.* 2008); see also chapter 2.3., Supplementary Material p.83, for an application of this version]:

$$F = \frac{F_{max}\,N}{N_0 + N} \qquad (1.6.10),$$

Hence, in analogy to equations (1.6.2; 1.6.3 and 1.6.4), a dynamic predator-prey model comprising non-linear interaction strength represented by the functional response F, would be, in its simplest form:

$$\frac{dN}{dt} = \alpha N\left(\frac{1-N}{K}\right) - FP \qquad (1.6.11),$$

and

$$\frac{dP}{dt} = FP - \delta N \qquad (1.6.12),$$

where the constant and linear interaction terms β and γ are substituted by F (see chapter 2.3., p.83, for a detailed version of this predator-prey model).

Apart from the dynamic population modelling, the particular shape of the non-linear density-dependence of the feeding rate has profound effects on the stability of the predator-prey relationship (Murdoch & Oaten 1975) where pure type-II responses (i.e., $q = 0$) tend to promote unstable equilibria and researchers have been looking for conditions favouring type-III responses for decades [e.g., (Hassell, Lawton, & Beddington 1977; Sarnelle & Wilson 2008); see next chapter on biological mechanisms creating type III effects]. There are two recent issues with far-reaching consequences that have to be highlighted when talking about sigmoid responses: (1) they are statistically difficult to detect in experiments and often are overseen due to inadequate experimental design (Sarnelle & Wilson 2008) and (2) stabilising effects on population dynamics do not only occur for values $q \geq 2$ but for values as small as 0.1 ~ 0.3 (Williams & Martinez 2004b; Rall *et al.* 2008).

b) Functional responses and biological mechanisms

Besides the theoretical and population-level considerations about functional responses there is a large body of empirical studies on the topic [see (Jeschke, Kopp, & Tollrian 2004; Englund *et al.* 2011; Rall *et al.* 2012) for reviews]. There, the functional response framework is widely applied to organisms from unicells [e.g., (Hewett 1980)] to whales [e.g., (Smout & Lindstrøm 2007)]. Consequentially and logically, these huge size differences require different observational and statistical approaches: While the study of large vertebrate functional responses usually implies fitting observational field data including information on interactions as well as abundance [e.g., wolf-moose (Messier 1994) or fish-fish predation (Kempf, Floeter, & Temming 2008)] the majority of empirical studies work with invertebrates in laboratory environments (Jeschke *et al.* 2004; Rall *et al.* 2012). The great advantages of laboratory studies in this context are obvious: controlled conditions allow to exclude environmental effects such as changing temperature (Englund *et al.* 2011; Vucic-Pestic *et al.* 2011; Rall *et al.* 2012) and a systematic setting up of experimental prey densities to avoid overlooking density-dependence of the capture rate (Sarnelle & Wilson 2008). On the other hand, there is the risk to deploy oversimplified environmental conditions [e.g., a typical setting in many biocontrol studies includes a tiny leaf or paper disk within a Petri dish, e.g., (Koch *et al.* 2003)] that cause overestimation of feeding rates compared to more complex and nature-near microhabitats (Munyaneza & Obrycki 1997; Hohberg & Traunspurger 2005). Furthermore, as prey refuge has been repeatedly related to density-dependent capture rates and type-III responses (Crawley 1992; Koen-Alonso 2007; Kempf *et al.* 2008) I used natural microhabitat structure (moss or leaf litter) in all the experiments in this thesis.

To understand the application of the functional response framework in the conceptual approach of this thesis, one has to regard the mechanistic meaning of its parameters: Particularly, the handling time depends on the context of the data: If predator satiation cannot be reached within the experiment [short-term functional response experiments, e.g., (Hjelm & Persson 2001)] than the *fitted* handling time will not include digestion time. Furthermore, studies that determine handling time by observation will come to other results than studies employing statistical fitting of handling times (Schenk & Bacher 2002), as other physiological processes are probably involved. Therefore, as the standard experimental time in all the experiments in this thesis was 24 hours where the predators could reach fully satiated conditions at high enough prey densities the following components are embraced in the fitted handling times in all studies

within this thesis: killing, ingestion and digestion of the prey, as well as resting and cleaning activities [see (Jeschke, Kopp, & Tollrian 2002) for a comprehensive and detailed discussion of the components of capture rates and handling times]. Secondly, the capture rate as a searching velocity describes an efficiency term that is composed of an encounter rate and a success rate (Gergs & Ratte 2009). Finally, for the capture exponent transforming hyperbolic to sigmoid response curves several biological mechanisms have been discussed (Hassell *et al.* 1977), with adaptive behaviour [i.e., prey switching (Murdoch, Avery, & Smyth 1975)] and the limited availability of prey refuges (Crawley 1992; Koen-Alonso 2007) being the most accepted.

For the sake of completeness I want to mention shortly some considerations on functional responses beyond the type II and type III classification that have not been discussed yet. Although these models and the mechanisms involved do not play a role in the following chapters, I think their theoretical considerations are vital for the understanding of the approach: One important mechanism that is not considered within this thesis but has caused intensive debates over the past decades is predator interference that might reduce feeding rates significantly (Abrams & Ginzburg 2000; Rall *et al.* 2008; Kratina *et al.* 2009; Lang, Rall, & Brose 2012). Through the specific design of the studies I have excluded these and other mechanisms potentially altering the functional response, where even the additional presence of non-prey species might reduce the feeding rate of the predator (Kratina, Vos, & Anholt 2007). In choosing to employ very simplified laboratory experiments there was the ability to check accurately for body-size (chapters 2.1.- 2.4.) and habitat structure (chapter 2.5.) effects. In chapter 2.4. I used the simple allometric models derived from chapter 2.1. to test how they are suited to predict the outcome of the two-prey experiment.

1.7. A short outline of this thesis

I examined body-size effects on the strength of interactions between a diverse set of terrestrial arthropod predators. This research was motivated by three documented phenomena of food webs and predator-prey interaction strengths within these webs:

1. Regular patterns in size structure of natural communities are strikingly evident. This phenomenon has been examined extensively and has been documented for predator-prey interactions in all ecosystem types.

2. Complex systems like food webs should be highly unstable according to

theoretical considerations. There is evidence that empirical body-size relations work against this paradigm.

3. The way of how the body-size relation between a predator and its prey shapes the interaction qualitatively and quantitatively might be the key to the understanding of stability in size-structured communities.

Therefore it was the aim of the studies within this thesis to find evidence for stabilising criteria in predator-prey interactions along a gradient of body-size ratios. Additionally, as I was interested particularly in the mechanisms that might create sigmoid functional responses, I also looked at potential prey refuge effect in structured habitats and if there might be stabilising effects.

I want to stress that the interaction models presented in this thesis should rather be seen as mechanistic null models and that I would not claim their absolute predictive power for specific interactions in nature [i.e., a simplifying rather than a summarizing model, sensu (Roughgarden 1983)]. Instead, I suggest to (1.) recognise the potential of body size as an easy-to-measure yet ubiquitous quantitative trait of a majority of living organisms and (2.) use deviations from allometric models for specific interactions and between specific systems as resources to understand the puzzling complexity of natural communities and their ways to exist through space and time.

1.8. Contributions to the included articles

Chapter 2.1: Allometric functional response model: body masses constrain interaction strengths

Authors: Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U.

Published in: Journal of Animal Ecology (2010), Vol. 79, pp. 249–256; doi: 10.1111/j.1365-2656.2009.01622.x

Idea by O.V.P, B.C.R. and U.B., laboratory work by all authors, statistical analyses by O.V.P & B.C.R., the text was written mainly by O.V.P., B.C.R. and U.B. with minor contributions of G.K..

Chapter 2.2: Taxonomic versus allometric constraints on non-linear interaction strengths

Authors: Rall, B.C., Kalinkat, G., Ott, D., Vucic-Pestic, O. & Brose, U.

Published in: Oikos (2011) Vol. 120, pp. 483–492; doi: 10.1111/j.1600-0706.2010.18860.x

Idea by B.C.R., G.K., O.V.P. and U.B., laboratory work by all authors; statistical analyses by B.C.R. & G.K.; the text was written mainly by G.K., B.C.R. and U.B. with minor contributions of D.O.; G.K. & B.C.R. contributed equally to this study.

Chapter 2.3: Generalised allometric functional responses facilitate predator-prey stability

Authors: Kalinkat, G., Schneider, F.D., Guill, C., Digel, C., Brose, U. & Rall, B.C. *Manuscript in preparation*

Idea and laboratory work by G.K., F.D.S., U.B. & B.C.R., statistical analyses by G.K., F.D.S. & B.C.R.; C.G. & C.D. provided analytical tools/new data, the text was written mainly by G.K., F.D.S., U.B. & B.C.R., with minor contributions of C.G. & C.D. G.K. & F.D.S. contributed equally to this study.

Chapter 2.4: The allometry of prey preferences

Authors: Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U.

Published in: PloS ONE (2011) Vol. 6 (10): e25937. doi:10.1371/journal.pone.0025937

Idea by G.K. & U.B., laboratory work by G.K. & O.V.P., statistical analyses by G.K., B.C.R. & U.B., the text was written by G.K., B.C.R. & U.B.

Chapter 2.5: Habitat structure alters top-down control in litter communities

Authors: Kalinkat, G., Brose, U. & Rall, B.C.

A revised version of this chapter is an article *in press* in: Oecologia; doi:10.1007/s00442-012-2530-6

Idea by all authors, laboratory work by G.K., statistical analyses by G.K. and B.C.R., the text was written by all authors.

2. Articles

2.1. Allometric functional response model: body masses constrain interaction strengths

a) Summary

1. Functional responses quantify the per capita consumption rates of predators depending on prey density. The parameters of these nonlinear interaction strength models were recently used as successful proxies for predicting population dynamics, food-web topology and stability.

2. This study addressed systematic effects of predator and prey body masses on the functional response parameters handling time, instantaneous search coefficient (attack coefficient) and a scaling exponent converting type II into type III functional responses. To fully explore the possible combinations of predator and prey body masses, we studied the functional responses of 13 predator species (ground beetles and wolf spiders) on one small and one large prey resulting in 26 functional responses.

3. We found (i) a power-law decrease of handling time with predator mass with an exponent of -0.94; (ii) an increase of handling time with prey mass (power-law with an exponent of 0.83, but only three prey sizes were included); (iii) a hump-shaped relationship between instantaneous search coefficients and predator–prey body-mass ratios; and (iv) low scaling exponents for low predator–prey body mass ratios in contrast to high scaling exponents for high predator–prey body-mass ratios.

4. These scaling relationships suggest that nonlinear interaction strengths can be predicted by knowledge of predator and prey body masses. Our results imply that predators of intermediate size impose stronger per capita top-down interaction strengths on a prey than smaller or larger predators. Moreover, the stability of population and food-web dynamics should increase with increasing body-mass ratios in consequence of increases in the scaling exponents.

5. Integrating these scaling relationships into population models will allow predicting energy fluxes, food-web structures and the distribution of interaction strengths across food web links based on knowledge of the species' body masses.

b) Introduction

Understanding constraints on species' interaction strengths is critically important for predicting population dynamics, food-web stability and ecosystem functions such as biological control (Berlow *et al.* 2004; Wootton & Emmerson 2005; Montoya, Pimm, & Sole 2006). Empirical and theoretical evidence suggests that predator and prey body masses are among the most important of these constraints (Emmerson & Raffaelli 2004; Wootton & Emmerson 2005; Woodward *et al.* 2005; Berlow, Brose, & Martinez 2008; Berlow *et al.* 2009). Conceptually, these nonlinear interaction strengths are described by the magnitude and shape of functional responses that quantify per capita consumption rates of predators depending on prey abundance. One generalized functional response model is based on Holling's disk equation (Holling 1959a):

$$F_{(N)} = \frac{bN^{q+1}}{1 + bT_h N^{q+1}} \qquad (2.1.1)$$

where F is the per capita consumption rate, N is prey abundance, T_h is the handling time needed to kill, ingest and digest a resource individual, b is a search coefficient that describes the increase in the instantaneous search rate, a, with resource abundance, N:

$$a = bN^q \qquad (2.1.2)$$

where q is a scaling exponent that converts type II into type III functional responses (Williams & Martinez 2004b; Rall *et al.* 2008). The hill exponent, h, used in some prior studies (Real 1977) is equivalent to q ($h = q + 1$).

Functional responses can be linear (type I, $T_h = 0$, increase up to a threshold abundance), hyperbolic (type II, $T_h > 0$, $q = 0$) or sigmoid (type III, $T_h > 0$, $q > 0$). While many early studies focused on type I and type II functional responses and ignored the scaling exponent, type III functional responses with scaling exponents larger than zero could occur more frequently than previously anticipated (Sarnelle & Wilson 2008). Under hyperbolic type II functional responses predation risks for prey individuals decrease with prey abundance causing inverse density-dependent prey mortality, which can lead to unstable boom-burst population dynamics (Oaten & Murdoch 1975aa; Hassell 1978). In contrast, increasing predation risks under sigmoid functional responses can yield an effective per capita top-down control that often prevents such unstable dynamics (Rall *et al.* 2008; Gentleman & Neuheimer 2008). Slight differences in functional response parameters can thus have drastic consequences for

population and food-web stability in natural ecosystems (Oaten & Murdoch 1975b; Williams & Martinez 2004b; Fussmann & Blasius 2005; Brose *et al.* 2006b; Rall *et al.* 2008).

Allometric scaling theories provide a conceptual framework how body masses could determine foraging interactions (Peters 1983; Brown *et al.* 2004). The maximum consumption rates realized at infinite prey densities are proportional to the inverse of handling time and independent of the success of the attacks (Yodzis & Innes 1992; Koen-Alonso 2007). Consequently, the 3/4 power-law scaling of maximum consumption with predator body mass (Peters 1983; Carbone *et al.* 1999) suggests that handling time should follow a negative ¾ power-law with predator body mass. This trend is qualitatively supported, though studies reported linear (Hassell, Lawton, & Beddington 1976; Spitze 1985), power-law or exponential relationships (Thompson 1975; Hassell *et al.* 1976; Aljetlawi, Sparrevik, & Leonardsson 2004; Jeschke & Tollrian 2005a).

The characteristic components of search rates include the reactive distance between predator and prey (i.e. the distance between predator and prey individuals at which a predator individual responds to the presence of the prey) and the capture success. While the reactive distance increases with the body masses of the predators (i.e. large predators have a larger visual range than small predators), the capture success decreases with predator mass above an optimum body mass ratio (Aljetlawi *et al.* 2004; Brose *et al.* 2008). A further explanation for the low capture success is that the predator's motivation to capture small prey of limited energy content is low (Petchey *et al.* 2008). Together, these patterns in reactive distances and capture success may explain the hump-shaped relationships between search rates and predator-prey body-mass ratios with a maximum search rate at intermediate (optimum) body-mass ratios documented in prior studies (Hassell *et al.* 1976; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Brose *et al.* 2008). However, these studies were either restricted to search rates of single predator–prey interactions (with variance in individual size) or studied multiple predator-prey search rates at a single, constant prey density. Thus, none of these prior studies has addressed body-size constraints on functional responses across species.

In this study, we quantified systematic effects of predator and prey masses on functional response parameters (handling time, search coefficient and scaling exponent) across different predator–prey interactions. While more complex functional response models accounting for digesting time and interference behaviour exist (Skalski & Gilliam 2001; Jeschke *et al.* 2002; Schenk, Bersier, &

Bacher 2005; Kratina *et al.* 2009), testing for their body-size dependence was left for subsequent studies. Instead, the allometric functional response model addressed here provide an empirical basis for an understanding of body-size constraints on interaction strengths, food-web topology (Petchey *et al.* 2008) and dynamics (Brose *et al.* 2006b; Otto *et al.* 2007; Rall *et al.* 2008; Brose 2008).

c) Methods

The predators of our experiment were carabid beetles (*Abax parallelepipedus*, *Carabus nemoralis*, *Pterostichus melanarius*, *Pterostichus oblongopunctatus*, *Harpalus rufipes*, *Calathus fuscipes*, *Calathus melanocephalus*, *Anchomenus dorsalis* and *Poecilus versicolor*; Carabidae: Coleoptera) and wolf spiders (*Trochosa terricola*, *Pardosa lugubris*; Aranea: Lycosidae) sampled in pitfall traps. The juvenile weight classes of 1, 3 and 10 mg of Trochosa were considered as trophic species as they vary in consumption rates and preferences for the different prey species (Rickers & Scheu 2005; Brose *et al.* 2008)(. We used *Alphitobius diaperinus* larvae (Coleoptera; Tenebrionidae; hereafter: *Alphitobius*), flightless adults of *Drosophila hydei* (Diptera; Drosophilidae, hereafter: *Drosophila*) and *Heteromurus nitidus* (Collembola; Entomobryidae, hereafter: *Heteromurus*) as prey.

Functional Response Experiments

To explore fully possible combinations in predator and prey body masses, we studied the functional response of each predator on one small and one large prey. For the beetles, we used flightless *Drosophila* as small prey and *Alphitobius* as large prey. For the spiders, we used *Heteromurus* as small prey and flightless Drosophila as large prey. Each experimental unit included one predator individual and prey at different initial densities that were varied between low densities (1, 3, 5, 10, 20, 30 prey individuals per experimental arena) and higher prey densities that were adjusted to each specific predator–prey combination to reach saturation in the predators per capita consumption rate (e.g. 120 individuals of *Drosophila* for the small predator *Anchomenus dorsalis* and 4000 individuals of *Drosophila* for the large predator *Carabus nemoralis*). Six replicates per prey density were established. The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for 1 week prior to the start of the experiments. The experiments were performed in Perspex® (Degussa AG, Darmstadt, Germany) arenas (20 x 20 x 10 cm) covered with lids that had holes to allow gas exchange. The ground was covered with

moist plaster (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.43 g dry weight) that was first dried for several days at 40°C to exclude other animals and then re-moisturised. The experiment was run for 24 h with a day/night rhythm of 12/12 h dark/light and temperature of 15°C. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape did not influence our experiments. The predators were weighed before and after the experiment to calculate the mean body mass of each predator and the body-mass ratio of each predator-prey pair (Table 2.1.1).

Statistical Analyses

In the present study, the prey densities changed during the experimental period with each consumption event. To account for this prey depletion during the experiments, we used a generalized model of Rogers's random predator equation (Rogers 1972; Juliano 2001):

$$N_e = N_0(1-\exp(bN_0^q(T_h N_e - T))) \quad (2.1.3),$$

where N_e is the number of prey eaten, N_0 is the initial prey density, b is the search coefficient (search rate $a = bN_0^q$), Th is the handling time, T is the experimental duration time and q is the scaling exponent. We fitted equation (2.1.3) to the experimental data using Newton's method in SAS 9.1 (Juliano 2001) to obtain parameter estimates. We prevented (i) negative scaling exponents (i.e. decreases in search rates with prey density) and (ii) negative handling times. Subsequently, we tested for effects of predator and prey masses on handling times, search coefficients and hill exponents. We used linear least-squares regressions to test for relationships between $\log_{10}$ handling time vs. $\log_{10}$ predator mass and $\log_{10}$ prey mass:

$$\log_{10} T_h = p \log_{10} M_P + n \log_{10} M_N + \log_{10} T_{h(0)} \quad (2.1.4)$$

with T_h as handling time, M_P as predator mass, M_N as prey mass, and p, n, $T_{h(0)}$ as constants. Hump-shaped relationships between $\log_{10}$-transformed search-coefficients, b, and predator–prey body-mass ratios, R, were tested by fitting the following size–search-coefficient curve in R (R Development Core Team 2010):

$$\log_{10}(b_{(R)}+1) = A\frac{\exp(\varepsilon(\Phi - \log_{10}(R+1)))}{1+\exp(\beta\varepsilon(\Phi - \log_{10}(R+1)))} \quad (2.1.5)$$

where A is a constant, Φ represents the body mass ratio at which 50% of the

maximum search coefficient is reached, ε is the rate of change in search with size controlling the steepness of the curve, R is the body-mass ratio and β determines the asymmetry of the curve (Vonesh & Bolker 2005). To find the optimum body mass ratio, R_0, where the maximum search coefficient is reached, the first derivative of equation (2.1.4) has to be set equal to zero and solved for R_0, resulting in the following equation (Vonesh & Bolker 2005):

$$\log_{10}(R_0+1)=\frac{\Phi+\log_{10}(\beta-1)}{\varepsilon\,\beta} \qquad (2.1.6).$$

The solution of equation (2.1.6) can be inserted in equation (2.1.5) to calculate the maximum search coefficient, $b_{max}(R_0)$.We tested for significant differences in scaling exponents, q, between predator-prey pairs using an ANOVA. Subsequently, we employed two contrast analyses (one for spiders and one for beetles) to test our hypothesis that the scaling exponent is higher for high predator-prey body-mass ratios (small prey) than for low ratios (large prey).

d) Results

Across the 26 functional responses of the present study (Table 2.1.1), we found substantial variance in search coefficients [$4.86 \leq b \leq 4.07$ x 10^3 (cm^2 day^{-1} ind^{-q} $Arena^q$)], handling times [$10^{-3} \leq T_h \leq 9.45 \cdot 10^{-1}$ (day $ind.^{-1}$)], and scaling exponents ($0 \leq q \leq 1.42$). In subsequent analyses, we related this variance in functional response parameters to predator–prey body-mass ratios spanning roughly three orders of magnitude from 0.65 to 532 (Table 2.1.1).

Table 2.1.1: Mean predator and prey weights, predator–prey body-mass-ratios, and functional response parameters: N = number of replicates, b = search coefficient (cm^2 day^{-1} ind^{-q} $Arena^q$), T_h = handling time (day ind.)1), SE = standard error, q = scaling exponent, weight = mean predator weight (mg) and R = predator–prey body-mass ratio

	N	b	SE	T_h	SE	q	SE	Weight	R
Beetles with large prey *Alphitobius diaperinus* [23.26 mg]									
Anchomenus dorsalis	3	0	0	0	0	0	0	14.50	0.65
Calathus melanocephalus	3	0	0	0	0	0	0	17.54	0.79
Calathus fuscipes	36	$9.33*10^2$	$1.39*10^{-3}$	0.52	0.07	0	0.0	71.52	3.08
Pterostichus oblongopunctatus	30	$3.88*10^3$	$1.27*10^{-2}$	0.62	0.06	0	0.0	69.65	2.99
Harpalus rufipes	48	$1.76*10^3$	$3.73*10^{-3}$	0.41	0.06	0	0.0	129.10	5.55
Pterostichus melanarius	36	$4.07*10^3$	$7.83*10^{-3}$	0.25	0.02	0	0.0	158.02	6.79
Abax parallelepipedus	24	$1.49*10^3$	$1.01*10^{-3}$	0.10	0.01	0	0.0	302.00	12.98
Carabus nemoralis	42	$2.98*10^2$	$8.62*10^{-4}$	0.06	0.02	0.11	0.7	513.14	22.06
Beetles with small prey Drosophila hydei [1.42 mg]									
Anchomenus dorsalis	57	$3.63*10^1$	$1.48*10^{-4}$	0.21	0.03	0.86	1.1	14.49	10.21
Calathus melanocephalus	57	$8.52*10^1$	$2.99*10^{-4}$	0.20	0.02	0.68	1	17.54	12.35
Calathus fuscipes	46	4.86	$2.00*10^{-5}$	0.10	0.01	1.42	0.8	81.82	57.62
Pterostichus oblongopunctatus	45	$2.53*10^1$	$7.60*10^{-5}$	0.12	0.01	1.08	0.7	65.05	45.81
Harpalus rufipes	54	$1.49*10^2$	$3.03*10^{-4}$	0.06	0.01	0.54	0.5	41.85	29.47
Pterostichus melanarius	54	$4.78*10^1$	$1.44*10^{-4}$	0.04	0.01	0.53	0.5	148.03	104.3
Abax parallelepipedus	90	$5.07*10^1$	$3.27*10^{-7}$	0.02	$2*10^{-3}$	1.41	0.7	287.58	202.5
Carabus nemoralis	76	$3.32*10^1$	$3.01*10^{-7}$	$5*10^{-3}$	0.01	0.68	0.7	463.84	326.7
Spiders with large prey Drosophila hydei [1.42 mg]									
Pardosa lugubris	54	$1.50*10^3$	$8.25*10^{-3}$	0.14	0.02	0.26	1.9	29.37	20.68
Trochosa terricola, 3 mg	42	$1.22*10^3$	$1.64*10^{-3}$	0.94	0.09	0	0	3.45	2.42
Trochosa terricola, 10 mg	36	$1.90*10^3$	$4.72*10^{-3}$	0.47	0.06	0	0	11.41	8.03
Trochosa terricola, adult	70	$2.07*10^2$	$4.71*10^{-4}$	0.03	$4*10^{-3}$	0.40	0.4	84.81	59.72
Spiders with small Heteromorus nitidus [0.15 mg]									
Pardosa lugubris	60	$1.27*10^1$	$3.90*10^{-5}$	0.05	0.01	1.10	0.6	25.77	171.8
Trochosa terricola, 3 mg	48	$3.43*10^2$	$6.76*10^{-4}$	0.10	0.01	0.5	0.7	3.08	20.51
Trochosa terricola, 10 mg	60	$1.27*10^2$	$3.25*10^{-4}$	0.02	0.01	0.40	0.5	10.61	70.75
Trochosa terricola, adult	88	$7.66*10^1$	$1.73*10^{-4}$	0.01	$1*10^{-3}$	0.10	0.3	79.79	532.4

The handling time exhibited a power-law decrease with in-creasing predator mass with an exponent of -0.94 ± 0.09 (mean ± SE, Fig. 2.1.1a) and a power-law increase with prey mass with an exponent of 0.83 ± 0.07. We caution, however, that these analyses are based on only three prey size classes and the latter exponent illustrates the relationship only qualitatively. Together, predator and prey mass explained 89% of the variation in handling time. The search coefficient followed a hump-shaped relationship with predator-prey body-mass ratios (Fig. 2.1.1b, r^2 = 0.74). The hump-shaped nature of this relationship depends on two data points with $\log_{10}$ mass ratios smaller than 0.5 (Fig 2.1.2b), but other predator species in this body-mass range have not been available. The maximum search coefficient, b_{max} = 2161.5, was reached at intermediate body-mass ratios of R_0 = 3.15 (i.e. predators are roughly three times larger than their prey). As handling time is proportional to the inverse of the predators' maximum consumption rates, the maximum nonlinear interaction strengths increase with the body-mass ratios (Fig 2.1.2). These maximum nonlinear interaction strengths are realized at the highest prey densities. At lower prey densities, the nonlinear interaction strengths also depend on successful search rates, which causes hump-shaped relationships with body-mass ratios (Fig. 2.1.2). The scaling exponent, q, was significantly higher for beetles and small prey (q = 0.89 ± 0.15, mean ± SE) than for beetles with large prey (q = 0.02 ± 0.11, Fig. 2.1.1c). This indicates that the nonlinear interaction strengths between beetles and their prey were best described by type-III functional responses for high predator–prey body-mass

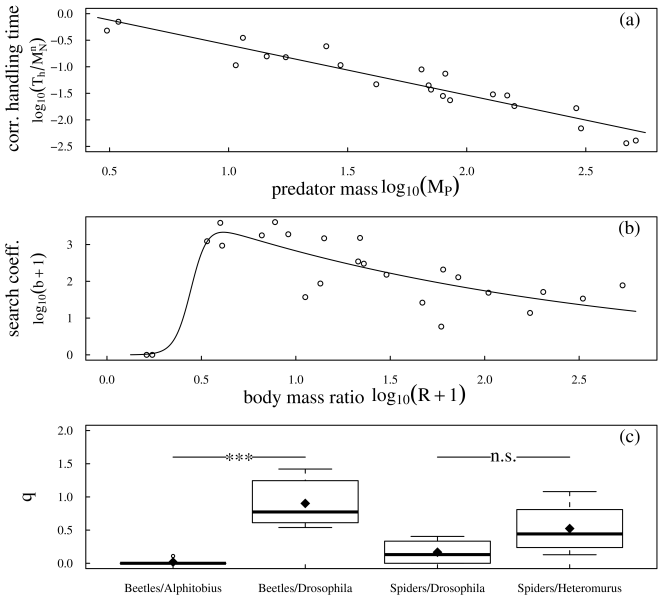


Figure 2.1.1: Allometric scaling of functional response parameters: **(a)** $\log_{10}$ handling time (min ind.$^{-1}$) decreases with $\log_{10}$ predator mass (mg); eqn (4): p = -0.94 ± 0.09 (mean ± SE, P < 0.001), n = 0.83 ± 0.07 (P < 0.001), $T_{h(0)}$ = 0.35 ± 0.14 (P < 0.01), r^2 = 0.887; note that handling time was normalized by the prey body-mass term in Eqn. (2.1.4): $\mathrm{corr}T_h = \log_{10}T_h$) $n\log_{10}M_N$; **(b)** search coefficients (cm^2 day^{-1} ind^{-q} Arena^q) follow a hump-shaped relationship with predator–prey body-mass ratios; eqn (5): A = 3.69 ± 0.52 (P < 0.001), ε = 0.48 ± 0.11 (P < 0.001), Φ = 0.45 ± 0.154 (P < 0.01) and β = 47.13 ± 88.67 (n.s.), r^2 = 0.74; **(c)** scaling exponents, q, and predator–prey pairs: Beetles / Alphitobius = low body mass ratio, Beetles / Drosophila = high body mass ratio, Spiders / Drosophila = low body mass ratio and Spiders / Heteromurus = high body mass ratio; significant differences among groups according to contrast analyses.

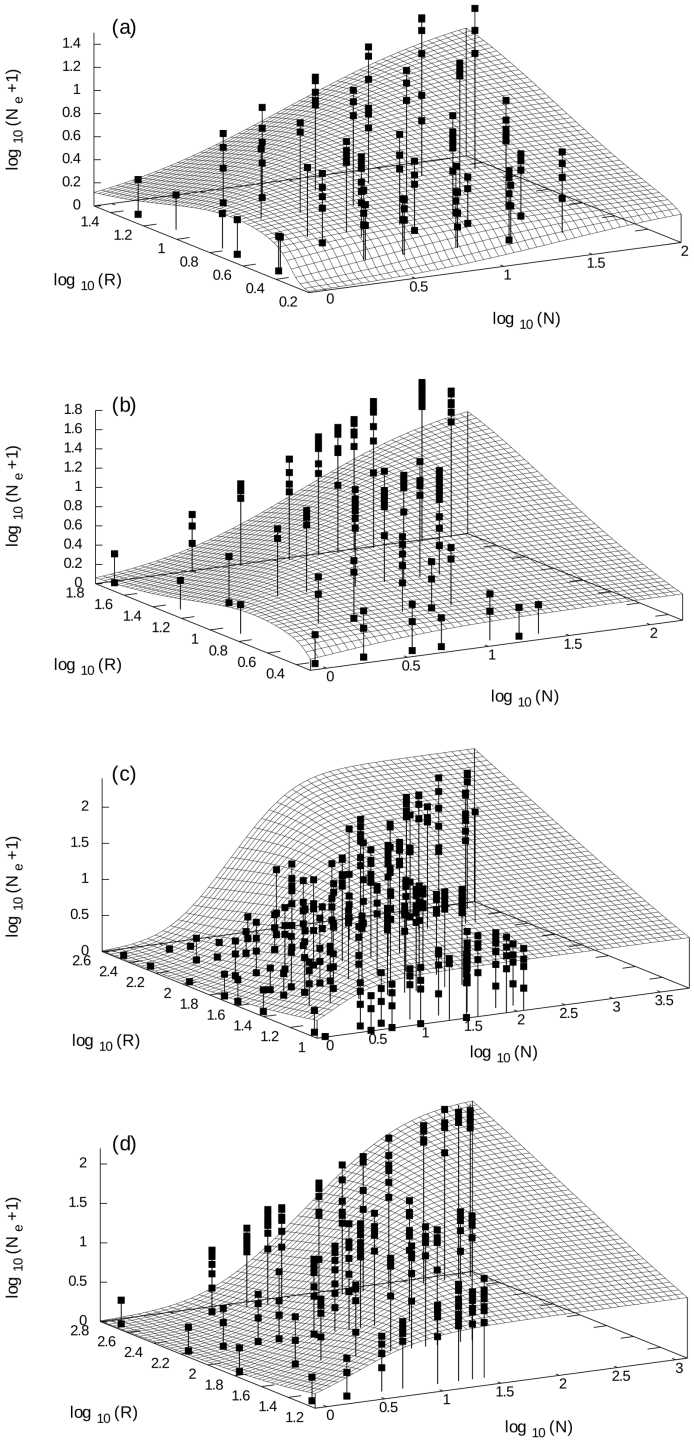


Figure 2.1.2: Experimental per capita consumption rates (N_e) depending on predator–prey body-mass ratios (R) and prey density (N) with allometric functional responses according to the allometric scaling functions of Fig. 2.1.1 for **(a)** Beetles / Alphitobius (low predator–prey body-mass ratios), **(b)** Spiders / Drosophila (low ratios), **(c)** Beetles / Drosophila (high ratios), **(d)** Spiders / Heteromurus (high ratios).

ratios when beetles fed on small prey (Fig. 2.1.2c), whereas type II functional responses characterized their interactions under low predator-prey body-mass ratios with large prey (Fig. 2.1.2a). While a similar pattern of type-III functional responses with small prey (high body-mass ratios; $q = 0.52 \pm 0.16$, mean ± SE) and type-II functional responses with large prey (low body-mass ratios; $q = 0.17 \pm 0.23$, mean ± SE) was found for spiders (Fig. 2.1.2d, b), this difference in the scaling exponent was not statistically significant (Fig. 2.1.1c, contrast analysis for spiders: $P = 0.17$).

e) Discussion

We studied the influence of predator and prey body masses on 26 functional responses of common terrestrial arthropod predators. We found: (i) power-law scaling in handling times with predator and prey masses, (ii) hump-shaped relationships between search coefficients and predator-prey body-mass ratios, and (iii) increases in the scaling exponent with body-mass ratios (only significant for beetles). Our findings provide evidence of how functional response parameters vary across predator-prey interactions of different body-mass ratios. We focused on two groups of generalist predators with different feeding strategies: beetles are mainly nocturnal, tactile and olfactory, whereas spiders are day active and optically oriented. The similarity in our findings for both predator groups suggests the broad generality of our results.

Interestingly, we found an exponent of -0.94 (SE = ±0.09) in the relationship between handling time and predator body mass, which is significantly different from the exponent of -0.75 initially predicted based on metabolic theory (Peters 1983; Yodzis & Innes 1992; Carbone *et al.* 1999; Brown *et al.* 2004). Thus, larger predators had lower handling times and smaller predators had higher handling times than expected based on metabolically driven processes. Assuming that metabolism mainly drives the digestive part of handling, it follows that the speed of morphologically constrained handling processes such as killing and ingesting the prey increases more steeply with predator mass than metabolic processes. For instance, if gut and stomach size are proportional to body size the maximum ingestion will also be proportional to body size. Consequently handling time should be inversely proportional to body size, which is consistent with our results. Consistent with most other functional response experiments, the short 24-h time period of our experiments thus emphasizes morphological over digestive constraints on handling times. An improved mechanistic understanding of the scaling exponents thus requires differentiating between ingesting and

digesting times in studies with varying experimental duration (Jeschke *et al.* 2002). While metabolic arguments suggest power-law scaling of digesting times with predator masses, ingesting times could be inversely proportional to body mass.

Instead of the expected linear increase in handling time with prey mass (exponent of unity), we found a scaling exponent of 0.83 ± 0.07 (mean ± SE). One plausible but speculative explanation for this difference could be that the energy content of the prey does not increase proportional to the prey mass. In this case, larger prey would contain more indigestible body parts (e.g. exoskeleton) that impose limitations on ingesting or digesting the prey body. However, a detailed analysis of the morphological and energetic structure of the prey biomass was beyond the scope of the present study. Moreover, we caution that our results were based on only two prey types for each of the predator groups, which may confound the prey-mass scaling relationships presented here. While our study demonstrates that handling time-scales with prey mass, subsequent studies should include a broader variation in prey body masses to more specifically address the exact exponent of this scaling relationship.

Consistent with prior studies investigating search coefficients at constant prey densities (Wahlström *et al.* 2000; Brose *et al.* 2008), our results corroborate the hump-shaped relationship between search coefficients and predator-prey body-mass ratios (Figs 2.1.1b and 2.1.2). While the present study was lacking data of direct behavioural observations, we follow prior studies in suggesting that the following behavioural constraints could be responsible for this hump-shaped relationship. Small predators (with low predator-prey body-mass ratios) have a small search area, and they have difficulties in subduing prey larger than themselves leading to inefficient attacks. Large predators (with high predator-prey body-mass ratios) have difficulties in catching small prey individuals, since the much smaller prey have faster reaction times and high escape efficiencies (Brose *et al.* 2008). At intermediate predator-prey body-mass ratios, however, the highest search coefficients were found, because predators are less restricted in subduing or catching the prey individuals. While the hump-shaped scaling of search coefficients with predator-prey body-mass ratios is supported by our data, these behavioural constraints remain hypotheses to be tested.

In our study, the two different predator groups were most efficient at a predator-prey body-mass ratio of R_0 = 3.15 (i.e. when predators were roughly three times larger than their prey). In a prior study, however, the group-specific capture mechanism of predators (e.g. sit-and-move vs. chasing predators) was

shown to have a large effect on the optimum predator-prey body mass ratio (Troost, Kooi, & Dieckmann 2008) suggesting that the optimum body-mass ratio documented here for epigeic spiders and beetles should not necessarily apply to other predator groups. Interestingly, in other ecosystems, a negative relationship between prey density and search rates could occur if the prey employs group defence mechanisms such as swarming (e.g. mammals or fish) (Jeschke & Tollrian 2005b). With respect to defence mechanisms of prey, the prey type may thus also influence these scaling relationships.

Moreover, prior studies reported maximum search coefficients of differently sized perch at R_0 = 49.8 for planktonic prey of 0.5 mm and at R_0 = 78.9 for prey of 1 mm size (Wahlström *et al.* 2000), and R_0 = 103.1 for wolf spiders and R_0 = 83.1 for ground beetles in terrestrial ecosystems (Brose *et al.* 2008). These studies were based on the simplifying assumption of constant prey densities, whereas the present study overcame this assumption by varying prey densities to estimate search rates of functional responses. While our results support the predicted hump-shaped search rates under varying prey densities, they also demonstrate that optima in the search coefficients were realized at body-mass ratios of R_0 = 3.15, which is approximately one order of magnitude lower than the optimum body-mass ratios of a prior study with the same species (R_0 of 83.1 or 103.1; Brose et al. 2008). This difference suggests that studies at constant prey densities might yield inaccurate estimates of optimum body-mass ratios. Interestingly, the optimum body-mass ratio of the present study is highly consistent with the geometric average body-mass ratio of 3.98 between invertebrate predators and their prey found in terrestrial food webs (Brose et al. 2006a). This implies that many interactions in terrestrial communities might be realized with maximum instantaneous search rates.

Consistent with prior studies, our results suggest that predators efficiently exploit prey within a specific size range. While our present results suggest that terrestrial predators are less specialized than previously anticipated (Brose *et al.* 2008), striking differences in optimum body-mass ratios, R_0, between these studies are evident. Disentangling whether these differences depend on the organisms investigated (e.g. beetles and spiders vs. fishes) or on ecosystem characteristics (terrestrial vs. pelagic) would require additional studies of varying predator groups in different ecosystem types. Eventually, these studies will allow addressing evolutionary and ecologically relevant questions of different optimum body-mass ratios and degrees of specialization across organism groups and ecosystem types.

In this study, we present evidence from systematic laboratory experiments that the scaling exponent, q, may increase with the predator-prey body-mass ratio, though this difference was only significant for ground beetles. This corroborates prior findings that type III functional responses could occur more frequently than previously anticipated (Sarnelle & Wilson 2008). Interestingly, a similar increase in the scaling exponent with prey size was reported based on gut content analysis of marine minke whales (Smout & Lindstrøm 2007). Together, these results could indicate a potentially broad universality of increases in scaling exponents with predator-prey body-mass ratios across different ecosystems.

It has been stressed that functional response experiments should apply a realistic habitat structure in the experimental arenas to create more natural experimental settings, since prey density often also relates to habitat structure (Real 1977; Crawley 1992). Moreover, it was hypothesized that adding such habitat structure could lead to a change of the functional response type as a consequence of potential hiding refuges for the prey (Real 1977; Hassell *et al.* 1977; Crawley 1992). Accounting for this fact, our experimental design included a constant density of moss as a natural habitat structure. Certainly, it would be important to replicate the functional responses of the present study across different moss densities to address how the body-mass effects documented here interact with effects of habitat complexity. Thus, the scaling exponents and attack coefficients of the present study should be interpreted only qualitatively, because different levels of habitat complexity should affect the absolute values of these parameters.

As a general, qualitative pattern, we found that this moss provided refuges for small prey from predation by large predators (high body-mass ratios) resulting in sigmoid, type-III functional responses with scaling exponents higher than zero. In contrast, predators of similar body mass as their prey (i.e. low body-mass ratios) were able to follow the prey into the hiding places within the habitat structure resulting in functional responses of type II with scaling exponents of zero. These observations during the experiments provide an explanation for the observed shift from functional responses of type II at low predator-prey body-mass ratios to functional responses of type III at high predator-prey body-mass ratios.

Interestingly, this suggests that population dynamics are stabilized by increasing body-mass ratios as a result of increasing scaling exponents (Oaten & Murdoch 1975a; b; Williams & Martinez 2004b; Brose *et al.* 2006b; Rall *et al.*

2008). While previous studies documented that high body-mass ratios stabilize population and food-web dynamics via reductions in the per unit biomass rates of metabolism and consumption (Emmerson & Raffaelli 2004; Brose *et al.* 2006a; Brose 2008), the increases in the scaling exponent documented here suggest an additional mechanism of how high body-mass ratios stabilize natural ecosystems.

We have presented the scaling of functional response parameters with predator and prey body masses with quantitative parameter estimates. This might be interpreted as an opportunity to estimate quantitatively functional responses based on body masses. However, we caution that this would be a misuse of our model: even in the case of the functional responses of the present study (Table 2.1.1) backward estimation of the per capita consumption rates based on the allometric functional response model yields substantial over- or under-estimations (Fig. 2.1.2). As other scaling models such as species-area relationships or metabolic scaling theory, the results presented here should be interpreted as a documentation of patterns across a body-mass scale. For instance, nobody would seriously estimate the species richness of Borneo based on a global species–area relationship, whereas this scaling model certainly has a tremendous value as conceptual cornerstone of biogeography. In the same vein, we suggest using the allometric functional response model presented here as an indication of scaling behaviour in foraging ecology. Integrating these scaling relationships into population models will allow predicting general trends in energy fluxes (Brose 2008), food-web structures (Petchey *et al.* 2008), and the distribution of interaction strengths across food-web links (Bersier, Banasek-Richter, & Cattin 2002). Eventually, combining allometric functional response models with those of food-web structure (Williams & Martinez 2000; Cattin *et al.* 2004; Petchey *et al.* 2008) may allow a more detailed understanding how the distribution of body masses across species in natural ecosystems determines population and food-web stability (Brose et al. 2006b; Otto et al. 2007; Rall et al. 2008).

2.2. Taxonomic versus allometric constraints on non-linear interaction strengths

a) Summary

Recently, the importance of body mass and allometric scaling for the structure and dynamics of ecological networks has been highlighted in several ground-breaking studies. However, advances in the understanding of generalities across ecosystem types are impeded to a considerable extent by a methodological dichotomy contrasting a considerable portion of marine ecology on the one hand opposite to traditional community ecology on the other hand. Many marine ecologists are bound to the taxonomy-neglecting size spectrum approach when describing and analysing community patterns. In contrast, the mindset of the other school is focused on taxonomies according to the Linnean system at the cost of obscuring information due to applying species or population averages of body masses and other traits. Following other pioneering studies, we addressed this lingering gap, and studied non-linear interaction strengths (i.e. functional responses) between two taxonomically-distinct terrestrial arthropod predators (centipedes and spiders) of varying individual body masses and their prey. We fitted three non-linear functional response models to the data: (1) a taxonomic model not accounting for variance in body masses amongst predator individuals, (2) an allometric model ignoring taxonomic differences between predator individuals, and (3) a combined model including body mass and taxonomic effects. Ranked according to their AICs, the combined model performs better than the allometric model, which provides a superior fit to the data than the taxonomic model. These results strongly indicate that the body masses of predator and prey individuals were responsible for most of the variation in non-linear interaction strengths. Taxonomy explained some specific patterns in allometric exponents between groups and revealed mechanistic insights in predation efficiencies. Reconciling quantitative allometric models as employed by the marine size-spectrum approach with taxonomic information may thus yield quantitative results that are generalized across ecosystem types and taxonomic groups. Using these quantitative models as novel null models should also strengthen subsequent taxonomic analyses.

b) Introduction

In ecology, a "classic" approach to understanding patterns and processes in communities and populations relies on description and measurement of traits, abundances and biological rates of species and interaction strengths between species defined by the Linnean taxonomic system. This traditional approach primarily characterises populations by their taxonomy while ignoring within-population variation in traits such as body mass, diet composition or habitat requirements. Still, this taxonomic approach has provided conceptual insights in structuring principles of natural communities including keystone species (Paine 1980; Power *et al.* 1996; Brose *et al.* 2005), phylogenetic constraints on the topology of food webs and pollinator networks (Cattin *et al.* 2004; Ives & Godfray 2006; Rezende *et al.* 2007; Bersier & Kehrli 2008), and mechanistic determinants of species' interaction strengths (Berlow *et al.* 1999, 2004; Otto *et al.* 2008). However, progress in the general understanding of population and community ecology is hampered by a lack of generality in these findings often tailored to the characteristics of specific taxonomically-defined species.

Empirical studies, however, revealed more complex allometric constraints on interaction strengths (i.e., functional responses - (Thompson 1975; Hewett 1980; Bence & Murdoch 1986; Wahlström *et al.* 2000; Woodward & Hildrew 2002b; Emmerson & Raffaelli 2004; Wootton & Emmerson 2005; Brose *et al.* 2008); see also chapter 2.1.) and regular body-mass distributions across species in natural food webs (Cohen *et al.* 1993; Woodward *et al.* 2005; Brose *et al.* 2006a). Employing these empirical relationships, food-web ecologists have made considerable progress regarding the long standing diversity-stability debate (McCann 2000; Montoya *et al.* 2006) by including body masses and allometric scaling into their scope (Berlow *et al.* 2008; Ings *et al.* 2009; Brose 2010). Analyses of food-web models demonstrated that allometric scaling relationships of metabolic rates and interaction strengths in combination with natural body-mass distributions yield stability of complex food webs (Emmerson & Raffaelli 2004; Brose *et al.* 2006b; Otto *et al.* 2007; Rall *et al.* 2008). The majority of the empirical food webs that were investigated in these studies rely primarily on taxonomic information applying species averages of the body mass, though sometimes populations are split into different "trophic species" [e.g. different live-stages of flatfishes in Emmerson and Raffaelli (2004)]. Obviously, such a procedure might obscure important information, particularly diet and trophic level shifts during ontogenesis of consumer individuals (Werner & Gilliam 1984; Polis 1991; Benton, Plaistow, & Coulson 2006; Arim *et al.* 2010).

Thus, it has been suggested to change the focus of community ecology from taxonomically-defined populations to size classes of individuals (Werner & Gilliam 1984; Ebenman 1989; Ings *et al.* 2009) to overcome the so-called "curse of the latin binomial" (Raffaelli 2007). However a "purely allometric concept" for the description of whole communities is currently mostly used in the field of marine ecology adopting a framework that characterizes individuals only by their body mass while any taxonomic information is discarded and individuals of distinct taxonomic groups are clustered into a discrete size classes. The conceptual backbone of this approach is provided by the size-spectrum theory [(Sheldon *et al.* 1972; Kerr 1974); reviewed in (Marquet *et al.* 2005)], which is successfully applied in empirical [e.g., (Jennings & Mackinson 2003; Blanchard *et al.* 2005)] and theoretical studies [e.g., (Blanchard *et al.* 2009; Law *et al.* 2009)] of pelagic systems. Despite its success in predicting community patterns, this exclusive focus on size classes of individuals comes at the cost of neglecting taxonomic or phylogenetic constraints on species' traits and interactions. In between these two extremes, some studies used intra-specific variation in body masses to explore their consequences for species traits, biological rates and population dynamics [e.g., (Persson *et al.* 1998; De Roos & Persson 2002; Persson *et al.* 2003; Rudolf 2006, 2008a; b; Rudolf & Armstrong 2008)]. Interestingly, one centrally important result documented that prey survival changes depending on both, predator identity and size (Rudolf & Armstrong 2008). However, we are not aware of any other study that directly compared the core assumption of size spectrum theory (i.e., "species' interactions depend on body mass but not on taxonomy"') against more taxonomically-oriented food-web and population ecology (i.e., "species' interactions depend on their taxonomy") with different taxa as well as body size ranging at both the consumer and the resource level. Aiming to fill this void, we adopted the functional-response model framework [(Solomon 1949; Holling 1959a); see below under Statistical Analyses for details] as a well-established metric of non-linear interaction strengths (Berlow *et al.* 2004) to address this question. So far, a plethora of functional responses between taxonomically-defined consumer and resource species have been studied while potential effects of variance in body masses amongst consumer and resource individuals were tested only in a small fraction of these studies [(Thompson 1975; Hewett 1980; Spitze 1985; Bence & Murdoch 1986; Hirvonen & Ranta 1996; Aljetlawi *et al.* 2004; Rudolf 2008b); see also chapter 2.1.]. Here, we expand these analyses by comparing whether *per capita* feeding data of terrestrial predators are better explained by a taxonomic, an allometric or a combined model.

c) Material and Methods

We compared taxonomic and allometric signatures in the functional responses of two predator species, the centipede *Lithobius forficatus* (Chilopoda: Lithobiidae; hereafter centipedes) and the wolf spider *Trochosa terricola* (Aranea: Lycosidae; hereafter spiders), on two prey species, the flightless fruit fly *Drosophila hydei* (Diptera: Drosophilidae; hereafter: fruit flies) and the springtail *Heteromurus nitidus* (Collembola: Entomobryidae; hereafter: springtails). We chose these two phylogenetically distant branches of arthropods, as chelicerata and myriapoda have been evolutionary separated for at least 500 million years (Pisani *et al.* 2004). Despite this phylogenetic difference, both predator groups share several common characteristics: (1) they are abundant in the same soil-litter habitats, (2) they occupy similar trophic positions, (3) they occur in similar body mass ranges, and (4) they employ a similar predation strategy of killing prey applying venoms (Chen & Wise 1999; Scheu & Falca 2000; Halaj, Peck, & Niwa 2005). For our study, spiders and centipedes were sampled by pitfall traps, and juveniles of both species were reared in the laboratory.

Functional response experiments

We studied the *per capita* feeding rates of centipedes and spiders by systematically varying (1) the body masses of both predators from smallest juveniles to adult individuals (body mass ranges from approximately 1.5 to 200 mg, the mean weight of before and after the experiment) and (2) the prey density (one to 120 individuals of fruit flies (1.42 mg) or one to 1000 individuals of springtails (0.15 mg)). This experimental design allowed addressing effects of taxonomy (spider versus centipede), predator body mass and prey-density on *per capita* ingestion rates.

The experimental set-up follows prior functional-response experiments [(Brose *et al.* 2008; Vucic-Pestic *et al.* 2011); chapter 2.1.] The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for at least 48 hours before the start of the experiments. The experiments were performed in Perspex® arenas (20x20x10 cm) covered with lids with gauze-covered holes to allow gas exchange. The arena floor was covered with moist plaster of paris (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.35 g dry weight) that was first dried for several days at 40°C to exclude other animals and then re–moisturised prior to the experiments. Prey

individuals were placed in the arenas half an hour in advance of the predators to allow them to adjust to the arenas. The experiment was running for 24 hours with a day/night rhythm of 12/12 h dark/light and temperature of 15°C in temperature cabinets. Initial and final prey densities were used to calculate the number of prey eaten. Control experiments without predators showed that prey mortality or escape was negligible.

Statistical Analyses

The taxonomic model

Following a taxonomic concept, we analysed the *per capita* feeding rates for each of the four predator-prey combinations (centipede - fruit flies, centipede - springtails, spider - fruit flies, spider - springtails). Different types of functional responses can be used to characterize *per capita* feeding rates depending on prey density. Following standard procedures, we first fitted a logistic regression model to the data of proportion of prey eaten versus initial prey density (Juliano 2001). This allows addressing whether the proportion of prey eaten continuously decreases (indicating a type II functional response) or follows a hump-shaped function (indicating a type III functional response, see Juliano (2001) for details). The results suggested the type-II functional response where a predator, i, feeds on a prey, j, with the parameters handling time, h_{ij} [h ind.$^{-1}$], and the instantaneous rate of successful attacks (hereafter: attack rate), a_{ij} [0.04m² h^{-1}], (Holling 1959a) as the most adequate model:

$$F_{ij} = \frac{a_{ij} N_j}{1 + a_{ij} h_{ij} N_j} \qquad (2.2.1),$$

where the *per capita* feeding rate of the predator, F_{ij}, depends on the initial prey density N_j. However, this model assumes a constant prey density throughout the experiment and has to be integrated over time and prey density (Royama 1971; Rogers 1972) yielding:

$$N_e = N_0 \left(1 - e^{a_{ij}\left(N_e h_{ij} - T\right)}\right) \qquad (2.2.2),$$

where N_e is the number of prey j eaten by predator i at the end of the experiment, N_0 is the starting density of prey j, T is the experimental time [h] and all other parameters are as in Eq. (2.2.1). We solved this recursive function of N_e with a non linear least squares method ("nls") using the additional package "emdbook" provided by Ben Bolker for the statistical software package R (Bolker

2008; R Development Core Team 2010). Additionally, the "nls" method allows to correct for grouping effects [(Ritz & Streibig 2009), pp. 109] such as the identity (ID) of predator and their prey. The resulting equation is

$$N_e = N_0 - \frac{W\left(a_{ij}\left[ID_{ij}\right]h_{ij}\left[ID_{ij}\right]N_0 e^{-a_{ij}\left[ID_{ij}\right]\left(T-h_{ij}\left[ID_{ij}\right]N_0\right)}\right)}{a_{ij}\left[ID_{ij}\right]h_{ij}\left[ID_{ij}\right]} \qquad (2.2.3),$$

where W is the Lambert W function (see Bolker (2008), pp. 268 and references therein for a detailed description). This approach of fitting a functional response with four groups for each parameter (h_{ij} and a_{ij}) results in eight free parameters. We will subsequently refer to it as the "taxonomic model".

The allometric model

Following the allometric concept, we did not differentiate between predator or prey taxonomy while fitting a single allometric functional response model to the *per capita* feeding data. Previous studies suggested that the parameters handling time and attack rate of functional responses follow allometric scaling relationships (i.e., they depend on predator and prey body masses - e.g., (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004); see also chapter 2.1.). These studies suggest that handling time, h_{ij}, should follow power law relationships with predator and prey body mass (chapter 2.1.):

$$h_{ij} = h_0 m_i^{c_i} m_j^{c_j} \qquad (2.2.4),$$

where h_0 is a constant, mi and m_j are the body masses [mg] of the predator i, and the prey j, respectively, and c_i and c_j are allometric exponents. Generally, attack rates follow hump-shaped relationships with predator-prey body-mass ratios [(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004); chapter 2.1.] While encounter rates generally increase with body masses as a consequence of increases in movement speed (Peters 1983), the success of the attacks decreases strongly at the highest predator-prey body-mass ratios (Gergs & Ratte 2009). To estimate the allometry of the attack rates, a_{ij}, we used a combined equation comprising a power law relationship for the prey body mass and an exponential Ricker function that describes a humped curve with increasing body mass ratios of the predator to the prey:

$$a_{ij} = a_0 m_j^{b_j}\left(R_{ij}\right)e^{\varepsilon\frac{m_i}{m_j}} \qquad (2.2.5),$$

where a_0 is a constant, m_j is the body mass [mg] of the prey j, R_{ij} is the body mass ratio of a predator to its prey ($R=\frac{m_i}{m_j}$), b_j is the exponent for the scaling of m_i, and ϵ is the exponential parameter determining the decrease of attack rates at high body mass ratios. To obtain the optimal body mass ratio where the attack rate is maximized, we differentiated Eq. (2.2.5) with respect to R_{ij} and set the resulting equation to zero. After solving this equation for R_{ij}, the optimal body mass ratio is: $R_{opt}=\frac{1}{-\varepsilon}$. Inserting R_{opt} into Eq. (2.2.5), yielding the maximum attack rate ($a_{ij}[R_{opt}] = A_{max}$).

This pattern of decreases and increases in attack rates at low and high prey body mass yields a hump-shaped attack model. As other hump-shaped models [(Persson *et al.* 1998; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Brose *et al.* 2008); chapter 2.1.] this model is purely phenomenological, but it has the advantage of mathematical feasibility in functional response models. Thus, inserting Eqs. (2.2.4 and 2.2.5) into Eq. (2.2.3) yields an allometric functional response model:

$$N_e=N_0-\frac{W\left(\left(a_0 m_j^{b_j}\left(R_{ij}\right)e^{\varepsilon R_{ij}}\right)\left(h_0 m_j^{c_j} m_i^{c_i}\right)N_0\, e^{-\left(a_0 m_j^{b_j}\left(R_{ij}\right)e^{\varepsilon R_{ij}}\right)\left(T-\left(h_0 m_j^{c_j} m_i^{c_i}\right)N_0\right)}\right)}{\left(a_0 m_j^{b_j}\left(R_{ij}\right)e^{\varepsilon R_{ij}}\right)\left(h_0 m_j^{c_j} m_i^{c_i}\right)} \quad (2.2.6).$$

This approach of fitting one allometric functional response containing six free parameters to the combined data set of all four predator-prey combinations will subsequently be referred to as the “allometric model”.

The combined model

Inserting the taxonomic groups into equation (2.2.6) results in a combined taxonomic and allometric model:

$$N_e=N_0-\frac{W\left(\begin{array}{l}\left(a_0[ID_i]R_{ij}e^{\varepsilon[ID_i]R_{ij}}\right)\left(h_0[ID_i]m_j^{c_j[ID_i]}m_i^{c_i[ID_i]}\right)*\\ N_0\, e^{-\left(a_0[ID_i]m_j^{b_i[ID_i]}\left(R_{ij}\right)\right)\left(T-\left(h_0[ID_i]m_j^{c_j[ID_i]_{m_i}c_i[ID_i]}\right)N_0\right)}\end{array}\right)}{\left(a_0[ID_i]m_j^{b_i[ID_i]}\left(R_{ij}\right)e^{\varepsilon[ID_i]R_{ij}}\right)\left(h_0[ID_i]m_j^{c_j[ID_i]_{m_i}c_i[ID_i]}\right)} \quad (2.2.7),$$

with 12 free parameters (each functional response parameter replicated for the taxonomic group of the predator).

All three models (Eqs. 2.2.3, 2.2.6, 2.2.7) can be converted into each other. Starting with the most complex combined model (Eq. 2.2.7) by removing the differentiation among predator identities results in the allometric model (Eq. 2.2.6). Alternatively, removing the terms of predator allometry from the combined model (Eq. 2.2.7) yields:

$$N_e = N_0 - \frac{W\left(a_0\left[ID_i\right] m_j^{b_j\left[ID_i\right]} h_0\left[ID_i\right] m_j^{c_j\left[ID_i\right]} N_0 e^{-a_0\left[ID_i\right] m_j^{b_j\left[ID_i\right]}\left(T - h_0 m_j^{c_j\left[ID_i\right]} N_0\right)}\right)}{a_0\left[ID_i\right] m_j^{b_j\left[ID_i\right]} h_0\left[ID_i\right] m_j^{c_j\left[ID_i\right]}} \quad (2.2.8).$$

In this model, the attack rates and handling times depend on predator identity and prey body mass. As we included only two prey species, the parameters prey identity and prey body mass are entirely redundant. Thus, the taxonomic model (Eq. 2.2.3) and the model of Eq. (2.2.8) are statistically equivalent, which implies that the combined model (Eq. 2.2.7) can also be simplified into the taxonomic model. Hence, the taxonomic (Eq. 2.2.3), and the allometric model (Eq. 2.2.6) can both be deduced from the combined model (Eq. 2.2.7), and the fit of all three models may be compared by their AICs.

d) Results

Under the taxonomic approach, the *per capita* feeding rates of all four predator-prey pairs followed a hyperbolic type-II functional response with marked differences in model parameters (Figure 2.2.1). Generally, both predators exhibited lower handling times and attack rates when preying on the smaller prey, springtails (Table 2.2.1). Interestingly, our results also suggest a phylogenetic difference in the functional responses: centipedes had a higher attack rate and a higher handling time than spiders when preying on fruit flies, whereas spiders had a higher attack rate and a higher handling time than centipedes when preying on springtails (Figure 2.2.1, Table 2.2.1). This suggests that spiders were able to ingest more fruit flies at high prey densities than centipedes (lower handling time of spiders), but centipedes were more efficient at low densities (higher attack rate of centipedes). The opposite result emerged for the smaller prey, springtails: the centipedes could ingest more prey individuals at high prey densities, but the spiders were more efficient at low prey densities. While six of all eight parameters of the functional response model were fitted significantly (the handling time for spiders feeding on Drosophila is almost significant (p = 0.058), substantial residual variation in *per capita* feeding rates

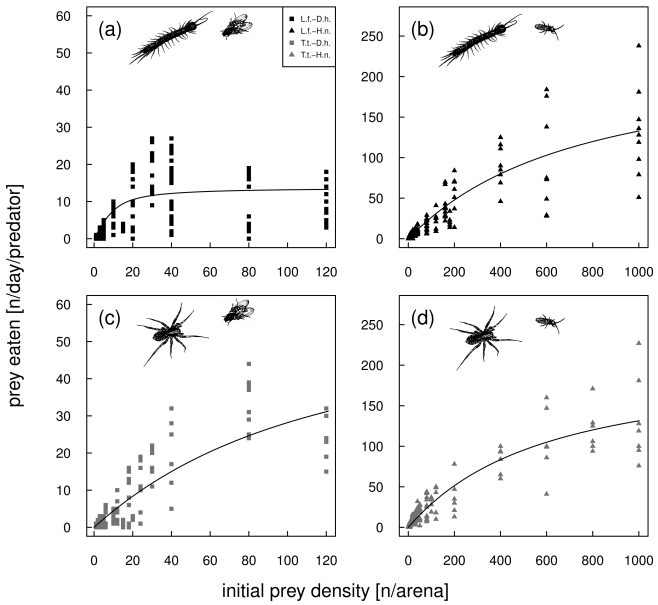


Figure 2.2.1: Taxonomic functional responses (Eq. 2.2.3) for **a)** centipedes feeding on fruit flies (black squares); (**b)** centipedes feeding on springtails (black triangles); (**c)** spiders feeding on fruit flies (grey squares); (**d)** spiders feeding on springtails (grey triangles). Note that we fit a single model to the data while disentangling the data in this figure for the sake of presentation. See Table 2.2.1 for model parameters.

remained (Figure 2.2.1). This unexplained variance in *per capita* feeding rates may be explained by the substantial variation in body mass of the predator individuals. The predator individuals were sampled in the field and represent the body-mass distribution of the natural populations: centipedes ranged from below ten mg to over 200 mg (Figure 2.2.2a), and spiders represented two cohorts (i.e., different life stages) with body masses between three mg and 160 mg (Figure 2.2.2b). The taxonomic model (Figure 2.2.1) is focused on taxonomic units while ignoring these differences in body masses among individuals (Figure 2.2.2).

Subsequently, we fitted an allometric model to the *per capita* feeding data that accounts for these differences in individual body masses while ignoring taxonomic variation amongst predators or prey (Eq. 2.2.6). Handling time followed a power-law decrease with predator body mass (Table 2.2.1). In consequence, both predators' feeding rates increased with predator body mass at high prey densities, where they are mainly driven by maximum feeding rates that are proportional to the inverse of handling time. Handling times on the larger prey, fruit flies, were significantly higher than on the small prey, springtails, as indicated by the significantly positive allometric exponent for prey body mass (Figure 2.2.3, Table 2.2.1). Also, the maximum attack rate is higher on larger prey than the attack rates on small prey (Figure 2.2.3, Table 2.2.1). The exponent, e, determining the shape of the Ricker function is negative, indicating a hump shaped function of the attack rate with increasing body-mass ratios of the predator to the prey with an maximal attack rate at a body-mass ratio of 553.8.

Subsequently, we fitted a combined model (Eq. 2.2.7) accounting for differences in prey and predator body-mass as well as predator taxonomy to the *per capita* feeding data (Fig. 4). This combined functional response model yielded decreases in handling time with predator body mass and increases with prey body mass (Table 2.2.1). The exponents scaling attack rates with prey body mass were positive (Table 2.2.1). The scaling parameter of the Rickers equation, ϵ, is less negative for centipedes than for spiders, indicating that larger centipedes are better in catching smaller prey than spiders (Table 2.2.1). These parameters result in an optimal body mass ratio of 648.7 for centipedes and 209.5 for spiders.

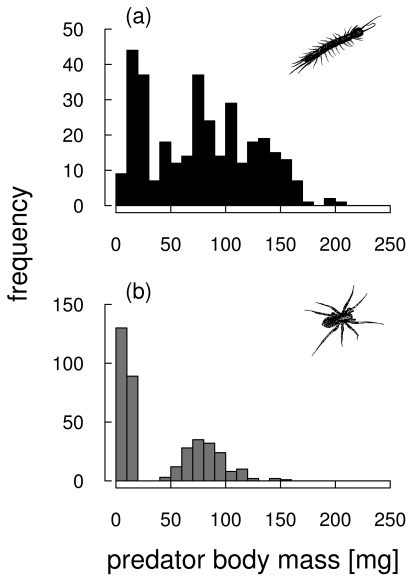


Figure 2.2.2: Distribution of individual body masses of **(a)** the centipede *Lithobius forficatus* (n = 333) and **(b)** the spider *Trochosa terricola* (n = 376). The predator individuals were sampled in the field and these data represent the natural body-mass distributions of the species.

The comparison of all three models (Figure 2.2.5) indicates a constant increase in the goodness of fit to the data. The higher feeding rates were well predicted by the taxonomic model and underestimated by the allometric model, whereas lower feeding rates where better predicted by the allometric than the taxonomic model (Figure 2.2.5a-b, high observed feeding rates on y-axis). The taxonomic model overestimated the data at low feeding rates substantially (Figure 2.2.5a). The combined model fitted the data of both, low and high feeding rates more adequately than the taxonomic or the allometric model (Figure 2.2.5a-c). In consequence, the taxonomic model has an AIC of 5776.2, the allometric model an AIC of 5706.3 and the combined model has an AIC of 5604.9 (Figure 2.2.5d, Table 2.2.1). Both, the taxonomic and the allometric model deviate significantly from the combined model (F-Test; allometric vs. combined: $p < 0.001$; taxonomic vs. combined $p < 0.001$).

Table 2.2.1: Parameters and standard errors (s.e.) estimated by the different functional response models (see Eqs. 2.2.3-2.2.7): the attack rate, a, with its parameters a_0, b_j and c; the handling time, h, with its parameters h_0, c_j, c_i. The optimal body-mass ratio R_{opt} and the maximum attack rate A_{max} (see Eq. (2.2.5) and its description in the methods).

Model	AIC	a	s.e.(a)	a_0	s.e.(a_0)	b_j	s.e.(b_j)	c	s.e.(c)	R_{opt}	A_{max} (springtails / fruit flies)
taxonomic	5776.2										
centipedes – springtails		0.014^{***}	0.0012								
centipedes - fruit flies		$0.130^{n.s.}$	0.1483								
spiders – springtails		0.017^{***}	0.0020								
spiders - fruit flies		0.026^{**}	0.0090								
Allometric	5706.3			0.0013^{*}	0.0006	1.38^{***}	0.2324	0.0018^{***}	0.0002	553.8	0.018 / 0.417
Combined	5604.9										
centipedes				$0.0019^{n.s.}$	0.0019	1.75^{***}	0.5158	0.0015^{***}	0.0002	648.7	0.016 / 0.833
spiders				0.0016^{*}	0.0007	0.60^{*}	0.2608	0.0048^{***}	0.0048	209.5	0.020 / 0.076
		h	**se(h)**	**h_0**	**s.e.(h_0)**	**c_j**	**se(c_j)**	**c_i**	**s.e.(c_i)**		
taxonomic											
centipedes – springtails		0.106^{***}	0.0100								
centipedes - fruit flies		1.741^{***}	0.3798								
spiders – springtails		0.118^{***}	0.0100								
spiders - fruit flies		$0.404^{\#}$	0.2125								
Allometric				4.22^{*}	2.00	1.07^{***}	0.067	-0.37^{***}	0.097		
Combined											
centipedes				$6.06^{n.s.}$	3.99	1.40^{***}	0.090	-0.41^{**}	0.135		
spiders				$22.94^{n.s.}$	19.73	0.82^{***}	0.097	-0.82^{***}	0.184		

e) Discussion

We studied the *per capita* feeding rates of two predators (centipedes and spiders) on two prey species (fruit flies and springtails) to compare the fit of three functional-response models: (1) a taxonomic model fitted to the four predator-prey pairs while ignoring differences in body masses between predator individuals, (2) an allometric model accounting for the body masses of predator and prey individuals while ignoring their taxonomy, and (3) a combined model accounting for differences in predator identity and the body masses of the predator and the prey individuals. Overall, our results suggest that the allometric model has a higher explanatory power than the taxonomic model. The combined model, however, improves the explanatory power over the allometric model, but it comes at the cost of containing twelve free parameters compared to only six free parameters of the allometric model. Despite this increase in parameter values, the combined model has the best AIC of all three models and is significantly different from the more simple taxonomic and allometric models.

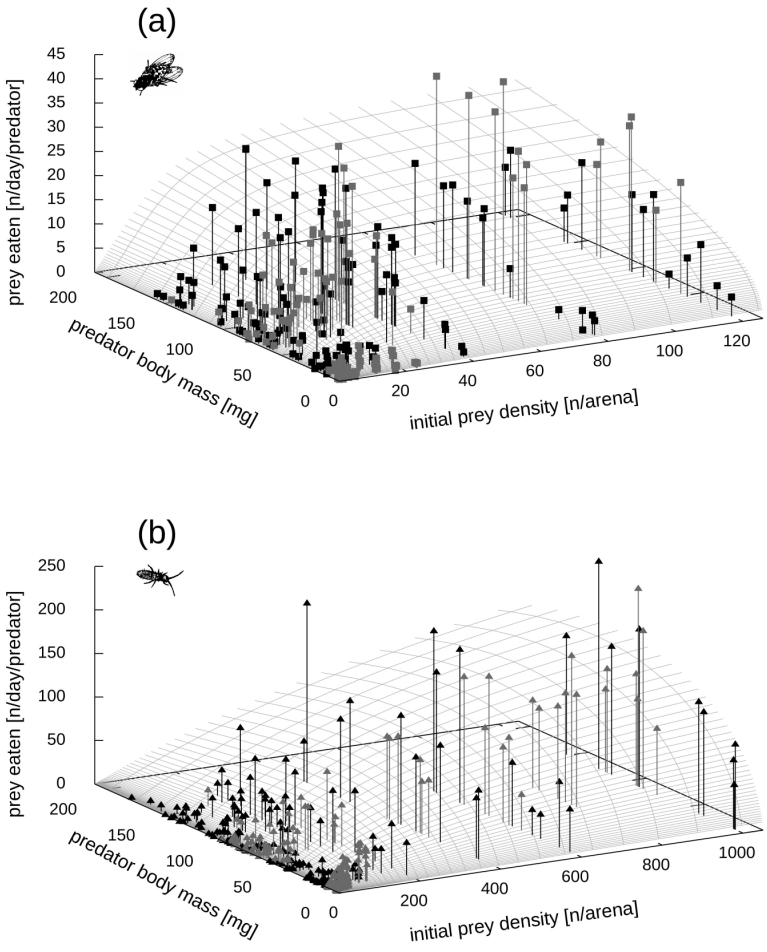


Figure 2.2.3: Allometric functional responses of both predator taxa (centipedes: black symbols; spiders: grey symbols) feeding on **(a)** *Drosophila hydei* and **(b)** *Heteromurus nitidus* (data fit by the allometric model). Note that we fit a single model to the data for both prey while disentangling the data in this figure for the sake of presentation. See Table 2.2.1 for model parameters.

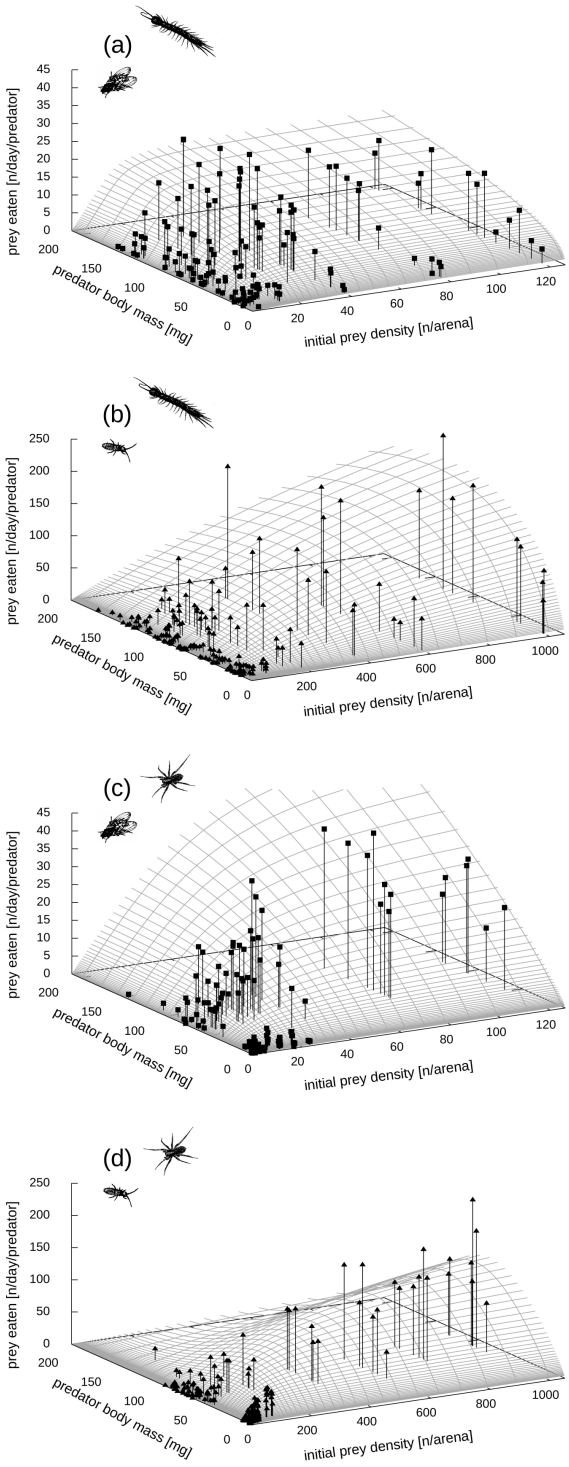


Figure 2.2.4: Combined taxonomic and body mass-dependent functional responses for **(a)** *Lithobius forficatus* feeding on *Drosophila hydei* (black squares); **(b)** *Lithobius forficatus* feeding on *Heteromurus nitidus* (black triangles); **(c)** *Trochosa terricola* feeding on *Drosophila hydei* (grey squares); **(d)** *Trochosa terricola* feeding on *Heteromurus nitidus* (grey triangles); data fit by the combined model. Note that we fit a single model to the data for both prey while disentangling the data in this figure for the sake of presentation. See Table 2.2.1 for model parameters.

In general, the allometric trends are similar in the allometric and the combined model and provide mechanistic explanations for trends in our taxonomic functional response parameters. First, the lower handling time and attack rates of both predators when preying on springtails is explained by its lower body mass compared to fruit flies. Secondly, we found a systematic power-law decrease in handling time with increasing predator body mass with exponents ranging from -0.37 (allometric) up to -0.83 (combined, spiders). This finding is explained by the higher metabolic capacity of larger predators whose maximum consumption rate (equal to the inverse of handling time) is directly proportional to their metabolic rate that often follows three-quarter power-law relationships with body mass (Brown *et al.* 2004; Brose *et al.* 2008; Rall *et al.* 2010). Thirdly, the allometric and the combined model yielded hump shaped attack rates with increasing body-mass ratios.

This finding is consistent with hump-shaped relationships of attack rates with increasing predator-prey body-mass ratio documented in prior studies (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004) as well as in chapter 2.1.. This pattern is driven by increasing encounter rates at low body-mass ratios as a consequence of increases in movement speed (Peters 1983), and strong decreases in the success of the attacks at high predator-prey body-mass ratios (Gergs & Ratte 2009). Together, these allometric scaling relationships yield the following pattern: at high prey densities, the maximum feeding rates follow power-law relationships with predator body mass as documented in prior ingestion studies from the laboratory up to the macro-ecological scale (Peters 1983; Carbone *et al.* 1999), whereas feeding rates at low prey densities are more constrained by the

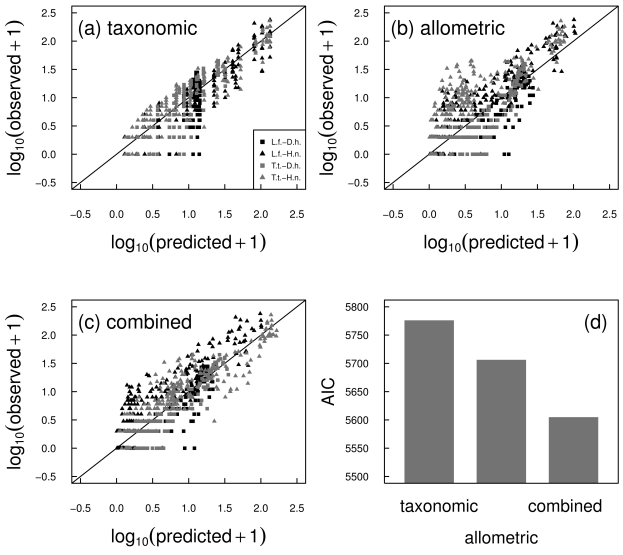


Figure 2.2.5: Goodness of fit comparison of all three models: **(a)** taxonomic model, **(b)** allometric model and **(c)** combined model. The empirically observed values of *per capita* feeding rates (y-axis) are plotted against the values predicted by the models (x-axis) using the statistically fitted parameters (see Fig. 2.2.1,2.2.3,2.2.4 for model parameters). The relationships in panels a-c indicate the overall coefficient of determination, AIC, of the models as shown in panel **(d)** (taxonomic = 5776.17, allometric = 5706.33, combined = 5604.93).

hump-shaped relationship between attack rates and predator-prey body-mass ratios. Similar patterns were also documented for terrestrial beetles in chapter, marine crustaceans (Aljetlawi *et al.* 2004), freshwater fly larvae (Spitze 1985), and freshwater fishes (Wahlström *et al.* 2000; Byström *et al.* 2003). However, even after accounting for effects of predator and prey body masses, significant differences among the predators remained. For instance, The optimal body-mass ratio (R_{opt}) for attack rates is 648.7 for centipedes, whereas for spiders it is 209.5, and centipedes attack fruit flies more efficiently than spiders (A_{max}; centipedes: 0.833, spiders: 0.076), whereas spiders had slightly higher maximum attack rates on springtails (A_{max}; centipedes: 0.016, spiders: 0.020). These results suggest that centipedes generally exploit fruit flies more efficiently than spiders at low densities when feeding rates are predominately driven by attack rates. However, spiders exploit springtails better than centipedes up to a body-mass ratio of 209.5. At higher body-mass ratios, the attack rates of spiders decrease due to an decreased capture efficiency, whereas centipedes have still increasing attack rates.

Both predator species in our experiments show a bimodal size distribution suggesting distinct size classes. However this is more a snapshot in time than a general phenomenon. Our approach of combining intra- and inter-specific variation in body masses to predict *per capita* feeding rates is certainly restricted to species that grow without changing hunting tactics. Additionally, our approach does not include more complex feeding interactions such as interference, cannibalism and intraguild predation that are important for the strength of an interaction over a longer period of time in natural populations. We anticipate that combining allometric functional-response models with these more complex feeding topologies will greatly improve our understanding of population and food-web stability in natural ecosystems. Due to logistic constraints our study was restricted to only two predator species when testing for taxonomic effect on interaction strengths. Subsequent studies will need to generalize our findings to data sets including more systematic variation in predator and prey taxonomy. The number of free parameters of the allometric model will be constant in such studies, whereas their number will increase with increasing predator and prey numbers for the combined and taxonomic models. We expect that the AIC of the combined model should increase in such studies, which might eventually lead to higher AICs compared to the more parsimonious allometric model. However, until these experiments are carried out this expectation remains speculative.

In summary, the allometric and the combined model provided a more

mechanistic insight in predator-prey interactions and achieved a higher explanatory power than the taxonomic model. Although prior studies did not compare such different model approaches statistically, they consistently documented allometric power-law scaling of handling time (see chapter 2.1.) and hump-shaped relationships between attack rates and predator-prey body-mass ratios (Spitze 1985; Wahlström *et al.* 2000; Byström *et al.* 2003; Aljetlawi *et al.* 2004; Gergs & Ratte 2009). This suggests that these general allometric relationships should hold across a broad range of taxa and body-mass distributions. Additionally, these results provide some evidence that the size-spectra approach employed in marine ecosystems (Sheldon *et al.* 1972; Kerr 1974; Jennings & Mackinson 2003; Jennings & Blanchard 2004; Blanchard *et al.* 2005; Andersen & Beyer 2006; Blanchard *et al.* 2009; Law *et al.* 2009) might also be applied to terrestrial ecosystems. Consistent with size-spectrum theory, we found that the *per capita* feeding rates appear to scale more strongly with individual body mass than with taxonomic differences. However, the combined model revealed statistical differences in the hunting efficiencies between the two predator groups. The most promising direction for future research thus reconciles quantitative allometric models with taxonomic effects. This will simultaneously yield quantitative allometric models generalized across taxonomic groups and mechanistic insights based on these quantitative models as novel null models for taxonomically-based analyses.

2.3. Generalised allometric functional responses facilitate predator-prey stability

a) Summary

The stability of ecological communities depends critically on the distribution and strength of interactions as quantified by non-linear functional responses. Two major approaches in community ecology have highlighted the importance of (1) classic functional-response types and (2) systematic constraints of body sizes on interaction strengths. Merging these two aspects of current food-web ecology, we present a novel framework with allometric constraints on all functional-response parameters including their type. To test this framework empirically we gathered the largest dataset on laboratory feeding rates of terrestrial invertebrates compiled so far. The predators and their prey cover a wide range of body-size ratios. Our results demonstrate that all functional-response parameters (i.e., handling times, capture coefficients and capture exponents) scale with predator and prey body masses. In consequence, our generalised functional responses replace the conventional functional-response types by an allometrically defined continuum from type II to type III at low and high predator-prey body-mass ratios, respectively. Subsequently, we implemented the generalised and the traditional functional responses in a bioenergetic model of population dynamics, which suggested stable coexistence for entirely different combinations of predator and prey body masses. Interestingly, an independent data set on terrestrial predator-prey interactions provided strong support for the predictions of the new generalised functional-response models. Together, these results suggest that the traditional functional-response types represent extremes of continuous allometric scaling functions. The novel generalised functional-response model presented here will allow a deeper understanding of quantitative interactions and their implications for the stability of food webs.

b) Introduction

The stability of populations, communities, and ecosystem functions depends critically on the strengths, distributions and characteristics of the interactions connecting species in complex food webs (de Ruiter, Neutel, & Moore 1995; McCann *et al.* 1998; Neutel *et al.* 2002; Rooney *et al.* 2006; Neutel *et al.* 2007). Traditionally, consumer-resource interactions have been categorised according to their functional response that most often describes hyperbolic (type II) or sigmoidal (type III) increases in the consumer's *per capita* feeding rate with the resource density (Holling 1959b; Oaten & Murdoch 1975b; Hassell *et al.* 1977; Jeschke *et al.* 2002, 2004; Sarnelle & Wilson 2008). While type-II functional responses generally lead to unstable, oscillatory dynamics, density-dependent *per capita* predation rates of type-III functional responses cause stable equilibria of population densities (Oaten & Murdoch 1975b; Williams & Martinez 2004b; Fryxell *et al.* 2007; Rall *et al.* 2008). However, characterising these functional-response types for each of the myriads of interactions in natural communities by tedious individual experiments is infeasible thus rendering a generalised understanding of natural population dynamics impossible.

An alternative approach employs body sizes and their "allometric" relationships with ecologically important traits of species and their interactions (Elton 1927; Sheldon *et al.* 1972; Peters 1983; Brown *et al.* 2004). This allometric approach predicts the biological rates of populations such as respiration, death and growth by population-averaged body masses (Peters 1983; Brown *et al.* 2004) that are often easily available for all consumer-resource pairs (Brose *et al.* 2006a). Moreover, this constrains the universe of possible combinations of biological rates into those that are probable given that they all scale with species' body masses (Brose 2010). While allometric models demonstrated that variance in consumer and resource body masses has profound effects on population dynamics (Yodzis & Innes 1992; Weitz & Levin 2006; Otto *et al.* 2007) and food-web persistence (Loeuille & Loreau 2005; Brose *et al.* 2006b; Rall *et al.* 2008; Brose 2008), they could not explain the radical dynamic shifts associated with differences between functional-response types, which limits their predictive accuracy.

Here, we present a novel approach merging allometric scaling models with functional-response types. These entirely allometric functional responses go beyond the traditional functional-response types by including allometric scaling relationships for the capture exponent shifting between functional-response

types. After fitting these allometric functional responses to a database of terrestrial predator-prey interactions, dynamical analyses demonstrate that these modifications of the functional responses cause severe differences in population dynamics. The resulting possible combinations of consumer and resource body masses enable stable coexistence. Finally, these differences are successfully tested against empirical consumer-resource body-size data from an entirely independent database.

c) Material and Methods

Functional responses

While there are various measures of interaction strengths (Berlow *et al.* 2004) the functional response model framework established by Solomon (1949) and Holling (1959b) has been used in a plethora of studies [reviews in (Jeschke *et al.* 2004; Englund *et al.* 2011)], where the *per capita* consumption rate of the predator, F, depends on the density of the prey, N:

$$F = \frac{a\,N}{1 + a\,h\,N} \qquad (2.3.1),$$

with the handling time, h, needed to kill, ingest and digest a prey individual (Jeschke *et al.* 2002) and the attack rate, a (hereafter: "capture rate"). This model framework is suitable for a wide range of consumer-resource interactions but as our experimental work was exclusively based on terrestrial invertebrate predators and their prey we will subsequently adhere to this terminology. Although there is only a limited number of functional-response studies that have been focussing on body-size relationships we now know that capture rates follow hump-shaped relationships with predator-prey body-mass ratio (e.g., (Hassell *et al.* 1976; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005); see also chapters 2.1. and 2.2.). while handling times generally decrease with increasing body mass ratios (Brose 2010), although different relationships have been reported (linear e.g., (Hassell *et al.* 1976; Spitze 1985), exponential or power law relationships e.g., (Hassell *et al.* 1976; Aljetlawi *et al.* 2004)]; see also chapters 2.1. and 2.2.). These relationships can be explained by allometric arguments provided by bioenergetic constraints (Yodzis & Innes 1992) and metabolic theory (Brown *et al.* 2004; Brose 2010).

The type-II functional response with a constant capture rate (Eq. 2.3.1) can be modified to account for capture rates that vary with prey density, $a = bN^q$ [(Real

1977; Williams & Martinez 2004b; Rall *et al.* 2008); chapter 2.1.] which yields type-III functional responses:

$$F = \frac{b N^{1+q}}{1 + b h N^{1+q}} \qquad (2.3.2),$$

where b is a capture coefficient (sometimes also referred to as search coefficient), and q is a scaling exponent (hereafter: capture exponent) that converts hyperbolic type-II (q = 0) into sigmoid type-III (q > *0*) functional responses [note that some authors refer to intermediate or modified type-II functional responses for values 0 < q < 1; e.g., (Williams & Martinez 2004b)]. Historically, the quest for type-III functional responses has been fuelled by its far-reaching consequences on population dynamics. Sigmoid functional responses promote stable equilibrium states as increasing predation risk can yield an effective per capita top-down control while at low population densities the prey is released from predation risk (Oaten & Murdoch 1975b; Yodzis & Innes 1992; Williams & Martinez 2004b; Rall *et al.* 2008). On the other hand the empirical and statistical documentation of type-III functional responses has been difficult (Sarnelle & Wilson 2008) and type-II functional responses prevail in the vast majority of laboratory studies (Jeschke *et al.* 2004). However, Sarnelle and Wilson (2008) showed that type-III functional responses might be more common than previously assumed and the lack of evidence for the existence of type-III responses might often be due to scanty replication at low prey densities. Another reason for a possible under-representation of type-III responses in laboratory studies might originate from oversimplified environment in experimental arenas lacking habitat structure that provides prey refuges especially for relatively small prey (Hassell *et al.* 1977; Crawley 1992). This concept has been confirmed by the study of Vucic-Pestic and colleagues (chapter 2.1.) where functional responses of predatory beetles and hunting spiders were tested for one large and one small prey species, respectively. There it has been shown that sigmoid type-III functional responses occur more likely when the predators feed on the smaller prey species (flightless fruit flies in experiments with beetles and springtails in experiments with spiders, respectively). Furthermore, the authors (chapter 2.1.) suggested a general allometric scaling of the capture exponent: increasing predator-prey body-mass ratios coincide with increasing values for q. Yet as only two prey sizes (that simultaneously represented two different prey species) per predator group where deployed in this study and a significant allometric relationship of the capture exponent was only documented for the beetles, the findings in chapter (2.1.) still have to be verified by a more generalised study

including more predator and prey groups and especially by extending the prey-size range. In the present study we therefore investigated the allometric effects on the functional response based on the data and the model framework developed in earlier studies[(Brose *et al.* 2008); chapters 2.1.and 2.2.]. While these studies only varied the size of the predator on a uniform prey, we now performed a series of experiments where predator *and* prey sizes were varied systematically. Subsequently, we combined results from previous and novel experiments to analyse the allometric relationships of capture rate, a, and capture coefficient, b, handling time, h, and the capture exponent q.

Feeding rate experiments

The basic experimental set-up mainly follows prior functional-response experiments [(Brose *et al.* 2008; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011); see also chapters 2.1. and 2.2.]. We studied the *per capita* feeding rates of 25 species of generalist arthropod predators (carabid and staphylinid beetles, lycosid, pisaurid and salticid spiders, centipedes) on eight differently-sized prey species varying initial prey densities from one to 1000 individuals of prey per arena (0.04 m²). Different life-stages of some of the predators were used to extend the body mass range (particularly *Trochosa terricola*, Aranaea and *Lithobius spec.*, Chilopoda). For most predators, we included only imagines, and for adult spiders only female individuals were used (see Supplementary Material, Table 2.3.B for a complete list of predator-prey pairs, their body-mass ratios and references to prior studies). We measured the body masses of each predator individual for each replicate individually. However, most replicates contained multiple prey individuals. Hence, we sorted prey individuals to minimize within-replicate variance in body mass and used the average prey body mass for each replicate (see Supplementary Material, Table 2.3.A for predator and prey species with body masses). Prey density levels were replicated up to eight times resulting in a total number of 2,820 experimental units. The predators were sampled from the field and only a small fraction of juvenile centipedes and lycosid spiders were reared in the laboratory until they reached the designated size class. The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for at least 48 hours before the start of the experiments. The experiments were performed in acrylic glass arenas (0.2×0.2×0.1 m) covered with lids with holes to allow gas exchange. The arena floor was covered with moist plaster of Paris (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.35 g dry weight) that was first dried for several days at 40°C to exclude other animals and

then re–moisturised prior to the experiments. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to disperse in the arenas. The experiments were run for 24 hours with a day/night rhythm of 12/12 h dark/light and temperature of 15°C in temperature cabinets. Initial and final prey densities were used to calculate the number of prey eaten. Predators were weighted before and after the experiments to calculate mean body mass. Control experiments without predators showed that prey mortality or escape was negligible.

Statistical analyses

Our general approach was based on fitting three different allometric functional-response models to the feeding-rate data that were evaluated according to their ΔAIC. The first model was a type-II functional response with fixed allometric-scaling exponents according to Yodzis and Innes (1992), where the capture rate

$$a = a_0 m_r^{-1} m_c^{0.75} \quad (2.3.3),$$

as well as the handling time

$$h = h_0 m_r m_c^{-0.75} \quad (2.3.4),$$

are described with h_0 and a_0 as constants and the body masses [g], m_c and m_r, of the predator c, and the prey r, respectively. These null models of allometric relations are based on the simplifying assumption that interaction parameters should scale with body masses as metabolic rate with a ¾ power law [(Peters 1983; Brown *et al.* 2004; Brose 2010), see Supplementary Material, p.80 for a detailed description of the derivation from the models in Yodzis and Innes (1992) into the allometric-scaling relations for Holling type-II functional-response parameters]. Subsequently, we will refer to this first model as traditional type-II functional response.

In the second model, allometric relationships were included according to prior studies (chapters 2.1. and 2.2.) where handling time, h, follows power law relationships with predator and prey body mass:

$$h = h_0 m_r^{c_r} m_c^{c_c} \quad (2.3.5),$$

where and c_c and c_r allometric exponents (see chapter 2.2.). As capture rates follow hump-shaped relationships with predator-prey body-mass ratios [(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004); chapter 2.1.] we estimated the

allometry of the capture rate, a, using a combined equation comprising a power-law relationship with prey body mass and an exponential Ricker function that describes a humped curve with increasing body-mass ratios of the predator to the prey:

$$a = a_0 m_r^{\beta_r} \frac{m_c}{m_r} e^{\varepsilon \frac{m_c}{m_r}} \quad (2.3.6),$$

where a_0 is a constant, β_r is the exponent for the scaling of m_r, and ε is the exponential parameter determining the decrease of capture rates at high body-mass ratios (see also chapter 2.2.). This pattern of decreases and increases in attack rates at low and high prey body mass yields a hump-shaped attack model [(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004); chapter 2.1.] We will refer to this second model as hump-shaped functional response.

Finally, we extended the second model by including sigmoid scaling of the capture exponent, q, with the predator-prey body-mass ratio R:

$$q = \frac{q_{max} R^2}{q_0^2 R^2} \quad (2.3.7),$$

where q_{max} and q_0 are scaling exponents defining the sigmoid relationship. The definition of the capture coefficient b (Eq. 2.3.2) then follows that of the capture rate (Eq. 2.3.6) substituting the constant b_0 for a_0:

$$b = b_0 m_r^{\beta_r} \frac{m_c}{m_r} e^{\varepsilon \frac{m_c}{m_r}} \quad (2.3.8).$$

Accordingly, the insertion of Eqs. 2.3.5, 2.3.7 and 2.3.8 into Eq. 2.3.2 yielded our third model (hereafter: generalised allometric functional response) accounting for hyperbolic as well as sigmoid forms of the response in dependence of predator and prey body masses.

To account for decreasing prey densities during experiments, we used the integrated form of the functional response, also known as Rogers' 'Random Predator Equation' (Royama 1971; Rogers 1972), for all three models:

$$N_e = N_0 (1 - \exp(a(N_e h - T))) \quad (2.3.9),$$

where N_e is the number of the prey eaten at during the experiment, T is the experimental time and all other parameters are as in Eq. (2.3.2) (with $a=bN^q$ in the generalised allometric functional response model scenario, see chapter 2.1.). We solved this recursive function of N_e with a non linear least squares method

("nls") using the additional package "emdbook" for the statistical software package R (Bolker 2008; R Development Core Team 2010). The resulting equation is

$$N_e = N_0 - \frac{W\left(a\,h\,e^{(a(hN_e - T))}\right)}{a\,h} \qquad (2.3.10),$$

where W is the Lambert W function (see Bolker (2008) and references therein for a detailed description).

Model analyses

To illustrate the consequences of these allometric relationships on population dynamics, we performed a series of simulations following a bioenergetic predator-prey model where the three scenarios of allometric relationships in the feeding interactions (the traditional type II, the hump-shaped and the generalised allometric functional response, respectively) were realised and other components of the model were also adjusted according to allometric constraints [(Yodzis & Innes 1992; Rall *et al.* 2008), see Supplementary Material, p.83 for methodological details of the model simulations]. Finally we compared the resulting persistence domains of the model simulations (i.e., the range of prey and predator sizes at which the predator is able to persist) with a novel data base on the consumer and resource body masses of terrestrial soil food webs from a large biodiversity research project in Germany [(Fischer *et al.* 2010), see Supplementary Material, p.85 for methodological details of data-base assembling].

d) Results

The comparison via AIC revealed that the generalised allometric functional response model with allometric scaling of all parameters including q was the best fitting model (ΔAIC = 0.0; degrees of freedom = 9) compared to the simpler, traditional type-II functional response (ΔAIC = 1703.74; df = 3) and the hump-shaped functional response (ΔAIC = 645.52; df = 7; see Supplementary Material,Table 2.3.F, p.82 for an overview of all parameters of the three fitted models). Together, these results imply that the novel generalised allometric functional-response model provides a substantially more accurate fit to the functional-response data, and all subsequent results will be based on this best-fitting model.

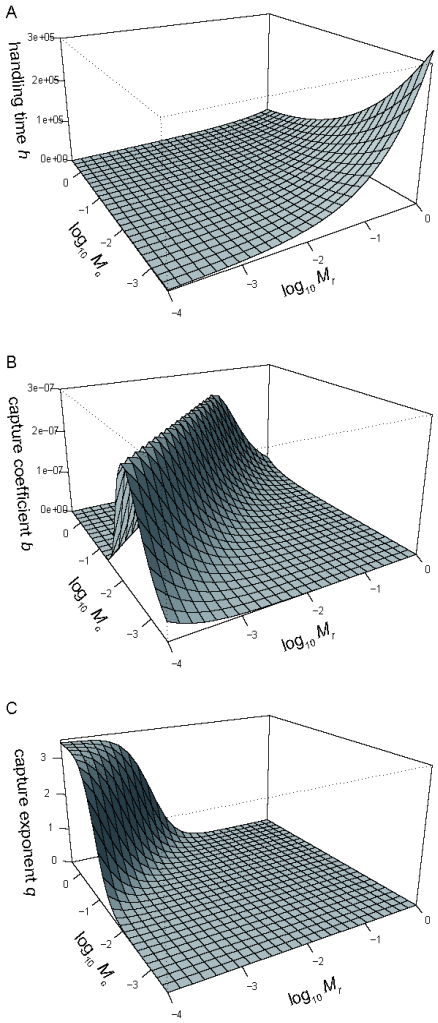


Figure 2.3.1: Relationship between the three fundamental functional response parameters handling time h **(A)**, capture coefficient b **(B)** and the capture exponent q **(C)** with $\log_{10}$ predator mass M_c [g] on the z- and $\log_{10}$ prey mass M_r [g] on the x-axis.

We found a negative power-law scaling relationship for handling time h with predator body mass ($h_0 = 35\,960$; standard error = 6 986; $p < 0.001$; $c_c = -0.2738$; s.e. = 0.0213; $p < 0.001$; Figure 2.3.1A), while h scaled positively with prey mass following a power-law relationship ($c_r = 0.544$; s.e. = 0.021; $p < 0.001$; Figure 2.3.1A). Hence, handling times follow power-law relationships with predator and prey masses resulting in highest handling times at very low predator-prey body-mass ratios (i.e., the prey is larger than the predator, Figure 2.3.1A). Furthermore, we found hump-shaped relations for the capture coefficient b with the predator-prey body-mass ratio ($b_0 = 1.212 \times 10^{-8}$; s.e. = 2.912×10^{-9}; $p < 0.001$; $\varepsilon = -0.0189$; s.e. = 0.0008; $p < 0.001$; Figure 2.3.1B) although the scaling factor β_r was not significant ($\beta_r = -0.0065$; s.e. = 0.0342; $p = 0.844$). This suggests that the capture coefficient did not scale explicitly with prey mass (besides the body-mass ratio scaling). Finally, the capture exponent q scaled positively with the predator-prey body-mass ratio R following a sigmoid relationship ($q_0 = 996.5$; s.e. = 19.83; $p < 0.001$; $q_{max} = 3.422$; s.e. = 0.144; $p < 0.001$; Figure 2.3.1C) implying that an increase in body-mass ratio causes a more sigmoidal functional response. This translates into type-II responses for small predators on relatively large prey, while large predators should be feeding on smaller prey following type-III responses according to the traditional categorisation of functional responses.

In Figure 2.3.2 (C and D) we illustrate how theses allometric constraints on functional-response parameters translate into specific feeding rates at fixed prey

(functional-response plane as a function of $\log_{10}$ predator mass, Figure 2.3.2C) and predator masses (functional-response plane as a function of $\log_{10}$ prey mass, Figure 2.3.2D). Figure 2.3.2A illustrates the location of these fixed body masses relative to the other data. In both graphs, the hump-shaped curvature for the feeding rates and the sigmoid behaviour at low densities and high body-mass ratios can be observed (Figure 2.3.2C,D). Additionally, Figure 2.3.2B provides an overview of the observed feeding rates in the experimental replicates versus the feeding rates predicted by the generalised allometric functional-response model.

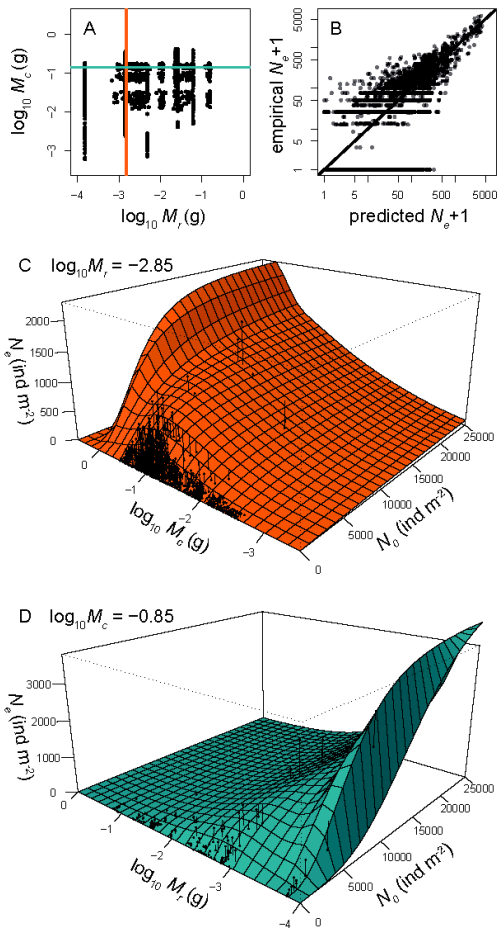


Figure 2.3.2: (A) Overview of the range of predator masses versus prey masses in the experimental replicates. The vertical, orange line (at $\log_{10} M_r = -2.85$) corresponds to the orange plane in Figure 2C while the blue horizontal line (at $\log_{10} M_c = -0.85$) corresponds to the plane in Fig. 2D; B-D) results for the best-fitting model, the generalised allometric functional response: **(B)** predicted feeding rates versus the observed feeding rates; **(C)** the functional response plane as a function of prey densities and $\log_{10}$ predator mass M_c at a fixed prey mass of $\log_{10} M_r = -2.85$; **(D)** the functional response plane as a function of prey densities and $\log_{10}$ prey mass M_r at a fixed predator mass of $\log_{10} M_c = -0.85$.

The results of the dynamic population model simulations under the three allometrically constrained feeding-rate scenarios are shown in Figure 2.3.3. There we show the persistence domains of the predator as a function of predator and prey body masses defined by the biomass-density minima [g m^{-2}] of the predator at the end of the simulations. While the predator in the model scenario based on the traditional functional response only persists with very low prey masses (Figure 2.3.3A), the other two model scenarios produce a more band-shaped persistence domain across the predator-prey masses (Figure 2.3.3B,C). However, these two domains exhibit pronounced differences including that under the hump-shaped functional-response model-scenario large predators can persist across a wide range of prey

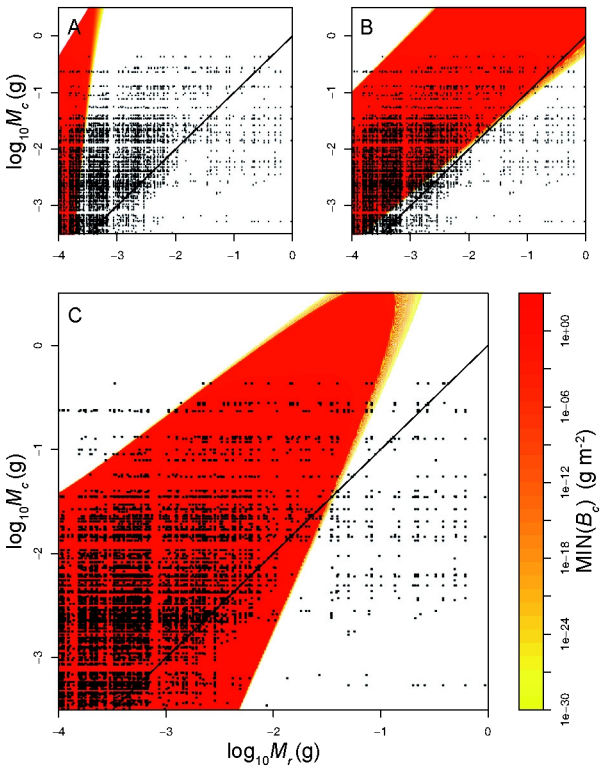


Figure 2.3.3: Results of the bioenergetic model simulations following three different functional response models: traditional type-II **(A)**; hump-shaped functional response **(B)** and generalised allometric functional response **(C)** (see Supplementary Material, pp.80 for parameter estimates of the three different models and pp.83 for the remaining parameter settings within the model simulations). Coloured planes represent the persistence domains of the predator shown as predator biomass density minima [g m^{-2}] as a function of $\log_{10}$ prey mass and $\log_{10}$ predator mass. Black dots represent empirical predator-prey interaction pairs from the Biodiversity Exploratories meta-food-web while the black diagonal represents the body-mass ratio $R = 1$ (i.e., where the mean size of the prey equals the mean size of the predator).

body masses (Figure 2.3.3B), whereas the generalised allometric functional-response model-scenario produces a cone-shaped persistence domain where the largest predators can only persist on a very small range of prey body masses (Figure 2.3.3).

Subsequently, we compared the persistence domains predicted by the dynamic population-models with empirical body-mass data of forest soil invertebrates. These data were chosen, because they include the same predator and prey groups as the functional-response experiments. We evaluated the models according to the percentage of natural predator-prey links (black dots in Figure 2.3.3A,B,C) that fall within the persistence domains. Interestingly, this comparison revealed that the fixed allometric-scaling relations following Yodzis and Innes (1992) yielded a persistence domain that included only 25.42 % of the natural body-mass combinations (Figure 2.3.3A), which is considerably less than the persistence domain of the hump-shaped functional-response model including 78.64 % of the interaction pairs (Figure 2.3.3B). The generalised allometric functional-response model performed best by yielding a persistence domain matching 95.57 % of the links in the food-web data base (Figure 2.3.3C).

e) Discussion

In the present study, we examined how the body masses of predators and prey constrain their interaction strengths. Corroborating prior functional-response studies [(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005); chapters 2.1. and 2.2.] we found power-law relationships between handling time and both predator and prey mass and hump-shaped relationships between capture rates and predator-prey body-mass ratios. In addition, our results go beyond previous studies by demonstrating that the capture exponent converting hyperbolic type-II into sigmoid type-III functional responses increases with predator mass and decreases with prey mass following a sigmoid function. Strikingly, this suggests that these classic functional-response types are not strict categories. Instead, our novel functional responses include gradual shifts from type-II predation of small predators on equally sized prey to type-III functional responses of large predators on small prey. This new paradigm of generalised allometric functional responses thus bridges lingering gaps between prior allometric models predicting quantitative interaction strengths and approaches based on functional-response types addressing constraints on population dynamics. Our bioenergetic model analyses illustrate entirely novel constraints of predator and prey body masses on population dynamics and persistence that deviate significantly from prior models. This new deepened understanding of population persistence is strongly supported by independent food-web data. Our results emphasise possible biological mechanisms that might be responsible for the regularities in body-size distributions across food webs (Brose *et al.* 2006a; Riede *et al.* 2011) with their critical importance for stability (Otto *et al.* 2007; Berlow *et al.* 2009).

General approach

Within the present study we have chosen an allometric approach by evaluating a large functional-response data base (more than 2,800 replicates) without accounting for the phylogenetic or taxonomic variance that the dataset comprises with 72 taxonomically different predator-prey pairs (Supplementary Material, Table 2.3.B). Previous work has shown how allometric functional-response models can (1) explain a large part of variation in predatory feeding rates with a minimal number of parameters as well as (2) be easily extended to account for taxonomic differences (see chapter 2.2.). We want to stress here that this kind of model has to be seen as a mechanistic baseline for our understanding of consumer-resource interactions and their implications for food-web stability.

While the traditional approach in research on interaction strengths has been to look at body-size constraints within the framework of taxonomic entities [e.g., (Hassell *et al.* 1976; Spitze 1985; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005)] we suggest to take allometry as a baseline and taxonomic (or phylogenetic) information atop following the concepts of the present study. Only until recently this approach was exclusively used in the aquatic sciences ["size spectra", e.g., (Sheldon *et al.* 1972; Jennings & Mackinson 2003)] but food-web ecologists have been calling lately for a more universal application of this approach (Raffaelli 2007).

Handling time and hump-shaped capture rates

Corroborating prior studies [(Hassell *et al.* 1976; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005); chapters 2.1. and 2.2.]we found (1) power-law increases in handling time with prey mass, (2) power-law decreases in handling time with predator mass, and (3) hump-shaped relationships between capture rates (i.e., capture coefficients) and predator-prey body-mass ratios. Metabolic arguments suggest that maximum consumption rates that are proportional to the inverse of handling time (Yodzis & Innes 1992; Koen-Alonso 2007) should follow the same scaling relationships with body mass as metabolic rates (Yodzis & Innes 1992; Brown *et al.* 2004). Interestingly, our results suggest that the power-law exponent of the relationship between handling time and predator mass (−0.27) is much shallower than the negative ¾ exponent expected by metabolic theory. Moreover, the power-law increase in handling time with prey mass is also shallower (0.54) than the expected isometric scaling. These shallow scaling relationships of handling time with predator and prey masses are corroborated by prior studies (chapters 2.1. and 2.2.). Together, these results suggest that handling time is constrained by more complex processes than metabolism. For instance, the scaling relationship for predator mass might be biased by different feeding modes such as sucking or chewing that shifts with increasing body masses (within our dataset) when comparing the feeding mode of liquid-feeding spiders (mean body mass: 0.036 g; n = 618) and centipedes (m.b.m.: 0.082 g; n = 903) on the one hand and the chewing beetles (m.b.m.: 0.124 g; n = 1299) on the other. Therefore small liquid feeders that ingest less unpalatable parts of their prey (e.g., sclerotised cuticle) than larger chewers ingesting whole prey items could account for shallower relationships.

Moreover, our results support previous studies showing a hump-shaped relationship between capture rates and predator-prey body-mass ratios

(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004); chapters 2.1. and 2.2.] Altogether, the qualitative check of the model with the observed versus predicted feeding rates (Figure 2.3.2B) shows that the model performs well at high feeding rates that are characterised by the handling time [i.e., proportional to the maximum ingestion rate (Koen-Alonso 2007)] whereas the model predictions overestimate especially the zero-consumption events (empirical $N_e + 1 = 1$, Figure 2.3.2B). Naturally, the model can hardly predict these cases where individuals do not feed at all. Although we controlled the most important factors that might cause the refusal of feeding (e.g., we standardised the hunger levels) there might be other biological mechanisms causing lowered foraging activity. For instance, spiders stop feeding several days before starting to moult (Foelix 1996).

Functional-response types

Historically, the majority of studies on sigmoid functional responses have been associated with prey switching[(Murdoch *et al.* 1975; Elliott 2006); chapter 2.4.]. whereas our study corroborates prior findings that type-III responses can come about in simple one predator – one prey systems [(Hassell *et al.* 1977; Sarnelle & Wilson 2008); chapter 2.1.]. There are diverse biological mechanisms that might be responsible for these allometrically-fostered sigmoid response curves. First, our experiments included habitat structure provided by moss to avoid overestimation of consumption rates that has been observed in unstructured artificial systems (Munyaneza & Obrycki 1997; Hohberg & Traunspurger 2005). It has been proposed that such conditions might provide prey refuges and that the existence of such refuges is suited to promote type-III responses [(Crawley 1992), p.53] particularly for large predator-prey body-mass ratios see chapter 2.1.). This concept is based on the assumption that large predators cannot follow their smaller prey into interstices provided by the moss. While a previous study (chapter 2.1.) demonstrated higher scaling exponents for larger predators, we generalised this concept across a wider range of predator and prey species with an extended range of prey sizes resulting in predator-prey body-mass ratios spanning roughly five orders of magnitude ($R_{min} = 0.08$; $R_{max} = 1\,199.50$, Supplementary Material, Table 2.3.B). Further mechanisms creating more sigmoid response curves might be explained by optimal foraging theory: Evolutionary fixed active enhancement (or reduction) in search effort at certain threshold levels of prey densities (Sih 1984) seem to be energetically reasonable. Especially at high predator-prey body-mass ratios it might not be profitable to pursue relatively small prey individuals at very low densities. This means that a predator would not “activate” its “foraging mode” aimed at small prey individuals

if their overall density was relatively small. Moreover, our approach of merging data on a wide range of predator-prey pairs to the unidimensional information of body masses together with the outstanding assemblage of the dataset (almost 3 000 experimental units) and an adequate replication at low initial prey densities assured detection of type-III behaviour following the suggestions of Sarnelle and Wilson (2008).

Previous theoretical studies have shown that slight changes in the capture exponent converting hyperbolic (i.e., type-II) into sigmoid (i.e., type-III) functional responses may have far-reaching consequences for population dynamics (Williams & Martinez 2004b; Rall *et al.* 2008) but a link between these concepts and allometrically constrained interaction strengths has been lacking so far. Hence, we present an allometric scaling of the capture exponent that is entirely novel. Interestingly, our results suggest that this capture exponent increases with predator-prey body-mass ratios thus suggesting hyperbolic and sigmoid functional responses at low and high body-mass ratios, respectively. This allometric concept goes beyond simple types of functional responses by relating a continuous distribution of functional-response shapes to the body masses of predators and their prey. Instead of fixed types, the shape of the functional response becomes an emergent property of predator and prey sizes.

Dynamic model

Consequences of these patterns on the level of populations are illustrated in Figure 2.3.3 where the results of the dynamic simulation module are shown for the complex model with the sigmoid scaling of q and the two simpler models: Firstly, the allometric null model of Yodzis and Innes (1992), where both capture rates and handling times follow power-law relationships with globally fixed scaling exponents results in a relatively small persistence domain where neither small nor large predators can persist on medium or large sized prey (within the size ranges investigated in the present study; Figure 2.3.3A). Meanwhile both allometric models with hump-shaped relation of the capture rates and capture coefficients, respectively, result in a persistence band within the predator-prey mass space (Figure 2.3.3B,C). Above all the comparison with the empirical food-web data shows that both the hump-shaped functional response (78.64 % of empirical predator-prey pairs within persistence domain) as well as the generalised allometric functional response (95.57 %) perform by far better than the traditional type-II functional response (25.42 %). The notable differences between the hump-shaped model from chapter 2.2. and our novel, generalised

model highlight the importance of the introduction of the additional, allometrically constrained component allowing for sigmoid response curves. This result is even more striking when taking into account that the persistence domain is smaller in the generalised allometric model. Interestingly, this also coincides with a particular pattern of body-size relations for the smallest predators: while the empirical data includes only a limited number of predator-prey pairs with a body-mass ratio $R<1$ (i.e., the predator is smaller than the prey; black dots beneath the black diagonal, Figure 2.3.3) the majority of these pairs are to be found for the smaller predators. This is the region within the predator-prey body-mass space where the hump-shaped functional-response model predicts significantly less of the natural predator-prey pairs than the generalised allometric functional response model.

Altogether, our analyses demonstrate how sigmoid response curves at high body-mass ratios contribute critically to the persistence of predator-prey relations. Moreover, we strongly suggest a replacement of the traditional view of functional response types by a concept of gradual transition between hyperbolic and sigmoid response curves framed by allometric constraints.

f) Conclusions

Within this study we add an essential upgrade to existing knowledge about how allometric effects on interaction strengths structure and stabilise ecological communities (i.e., food webs). Our approach included laboratory feeding-rate experiments, statistical modelling of allometric relations in the experiments, simulations of population dynamics according to our empirical findings and, finally, a comprehensive test of the theoretical implications based on an independent dataset of predator-prey interactions. The core message of our results comprises the advise to outstrip traditional functional-response types and rather replace this categorical thinking by an allometrically defined continuum of hyperbolic and sigmoid response curves. This suggestion has far-reaching consequences for our understanding of structure and stability of food webs as smaller predators feed with hyperbolic responses on their similarly sized prey whereas large predators feed on small prey according to sigmoid response curves. We outline the consequences of our findings with analyses of predator-prey population dynamics under different allometrically constrained interaction models. The persistence domain we found in these bioenergetic population simulations is of striking accordance with the empirical predator-prey pairs from an extensive and independent database. This underlines the importance of this

missing link between stability-promoting characteristics and allometric structuring of non-linear interaction strengths.

g) Supplementary Material

Predator and prey species and their body masses

Table 2.3.A: Species list with mean, minimum and maximum body masses [gram]

	number of replicates	mean mass	min mass	max mass
Predators				
Chilopoda				
Lithobius forficatus	903	0.08215	0.00657	0.20391
Coleoptera				
Carabidae				
Abax ovalis	105	0.16790	0.12151	0.24280
Abax parallelepipedus	176	0.30149	0.22000	0.41916
Anchomenus dorsalis	107	0.01448	0.00810	0.02160
Calathus fuscipes	36	0.07152	0.04525	0.11184
Calathus melanocephalus	6	0.01725	0.01145	0.02125
Calathus piceus	12	0.04492	0.03605	0.05625
Harpalus affinis	56	0.05078	0.03680	0.06590
Harpalus rufipes	142	0.11942	0.07635	0.19025
Nebria brevicollis	57	0.06589	0.04234	0.10365
Notiophilus biguttatus	44	0.00559	0.00400	0.00675
Notiophilus laticollis	40	0.00688	0.00459	0.00835
Poecilus cupreus	8	0.08784	0.08220	0.09740
Poecilus versicolor	140	0.06058	0.04015	0.08215
Pterostichus burmeisteri	27	0.10595	0.08495	0.12620
Pterostichus melanarius	110	0.15953	0.10984	0.26120
Pterostichus oblongopunctatus	122	0.06917	0.04765	0.08685
Staphylinidae				
Ocypus olens	70	0.30597	0.21644	0.40833
Ocypus ophtalmicus	18	0.08858	0.05198	0.11696
Philonthus fuscipennis	20	0.02250	0.01785	0.02970
Staphylininae	3	0.02980	0.02005	0.03910
Aranaea				
Lycosidae				
Alopecosa spec.	34	0.01974	0.00060	0.07115
Pardosa lugubris	139	0.02975	0.02000	0.09430
Pardosa palustris	12	0.02922	0.01945	0.06825
Pirata spec.	25	0.02669	0.01400	0.05905
Trochosa terricola	388	0.03983	0.00200	0.15425
Pisauridae				
Pisaura mirabilis	13	0.10242	0.07050	0.17025
Salticidae				
Salticus scenicus	7	0.00676	0.00150	0.03030

Prey					
Isopoda					
	Trichorhina tomentosa	108	0.00268	0.00067	0.00561
Collembola					
	Heteromurus nitidus	526	0.00015	0.00015	0.00015
Ensifera					
	Acheta domesticus	242	0.06303	0.00077	0.15987
	Gryllus sigillatus	54	0.00478	0.00478	0.00478
Coleoptera					
	Tenebrio molitor (Larvae)	118	0.06116	0.06116	0.06116
	Alphitobius diaperinus (Larvae)	363	0.01652	0.00104	0.03046
Diptera					
	Lucilia caesar (Larvae)	402	0.02604	0.02604	0.02604
	Drosophila hydei (Imago, flightless)	1007	0.00143	0.00143	0.00143

Table 2.3.B: Predator-prey pairs with mean body-mass ratios

predator	prey	number of replicates	mean body-mass ratio	published in
Alopecosa spec.	*Heteromurus nitidus*	16	141.167	Brose et al (2008)
Alopecosa spec.	*Gryllus sigillatus*	18	3.791	Brose et al 2008
Abax ovalis	*Drosophila hydei* (Imago, flightless)	60	112.830	unpublished
Abax ovalis	*Lucilia caesar* (Larvae)	39	6.849	unpublished
Abax ovalis	*Tenebrio molitor* (Larvae)	6	2.802	unpublished
Abax parallelepipedus	*Drosophila hydei* (Imago, flightless)	67	200.318	Vucic-Pestic et al
Abax parallelepipedus	*Lucilia caesar* (Larvae)	55	12.042	unpublished
Abax parallelepipedus	*Tenebrio molitor* (Larvae)	12	5.092	unpublished
Abax parallelepipedus	*Alphitobius diaperinus* (Larvae)	42	13.259	Vucic-Pestic et al (2010b)
Anchomenus dorsalis	*Drosophila hydei* (Imago, flightless)	72	10.150	Vucic-Pestic et al 2010
Anchomenus dorsalis	*Tenebrio molitor* (Larvae)	35	0.386	unpublished
Calathus fuscipes	*Alphitobius diaperinus* (Larvae)	36	3.075	Vucic-Pestic et al 2010
Calathus melanocephalus	*Drosophila hydei* (Imago, flightless)	6	12.107	Brose et al 2008
Calathus piceus	*Drosophila hydei* (Imago, flightless)	6	31.772	Brose et al 2008
Calathus piceus	*Lucilia caesar* (Larvae)	6	1.711	Brose et al 2008
Harpalus affinis	*Tenebrio molitor* (Larvae)	17	0.857	unpublished
Harpalus affinis	*Drosophila hydei* (Imago, flightless)	24	34.383	unpublished
Harpalus affinis	*Lucilia caesar* (Larvae)	15	1.989	unpublished
Harpalus rufipes	*Tenebrio molitor* (Larvae)	18	2.009	unpublished
Harpalus rufipes	*Drosophila hydei* (Imago, flightless)	78	81.471	Vucic-Pestic et al 2010
Harpalus rufipes	*Lucilia caesar* (Larvae)	46	4.750	unpublished
Lithobius forficatus	*Acheta domesticus*	242	21.162	unpublished
Lithobius forficatus	*Alphitobius diaperinus* (Larvae)	220	15.554	unpublished
Lithobius forficatus	*Drosophila hydei* (Imago, flightless)	144	54.354	Rall et al (2011)
Lithobius forficatus	*Heteromurus nitidus*	189	515.711	Rall et al 2011
Lithobius forficatus	*Trichorhina tomentosa*	108	37.748	unpublished
Nebria brevicollis	*Drosophila hydei* (Imago, flightless)	21	42.363	Brose et al 2008; unpublished
Nebria brevicollis	*Lucilia caesar* (Larvae)	36	2.654	Brose et al 2008; unpublished
Notiophilus biguttatus	*Drosophila hydei* (Imago, flightless)	37	3.981	Brose et al 2008; unpublished
Notiophilus biguttatus	*Lucilia caesar* (Larvae)	3	0.177	Brose et al 2008
Notiophilus biguttatus	*Tenebrio molitor* (Larvae)	4	0.090	unpublished
Notiophilus laticollis	*Drosophila hydei* (Imago, flightless)	33	4.989	Brose et al 2008; unpublished
Notiophilus laticollis	*Lucilia caesar* (Larvae)	3	0.198	Brose et al 2008
Notiophilus laticollis	*Tenebrio molitor* (Larvae)	4	0.103	unpublished
Ocypus olens	*Drosophila hydei* (Imago, flightless)	36	200.008	Brose et al 2008; unpublished
Ocypus olens	*Lucilia caesar* (Larvae)	34	12.603	Brose et al 2008; unpublished
Ocypus ophtalmicus	*Drosophila hydei* (Imago, flightless)	6	57.840	unpublished
Ocypus ophtalmicus	*Lucilia caesar* (Larvae)	12	3.520	unpublished
Pardosa lugubris	*Drosophila hydei* (Imago, flightless)	63	22.245	Vucic-Pestic et al 2010

Pardosa lugubris	*Heteromurus nitidus*	70	181.076	Vucic-Pestic et al 2010
Pardosa lugubris	*Gryllus sigillatus*	6	8.281	Brose et al 2008
Pardosa palustris	*Heteromurus nitidus*	6	174.444	Brose et al 2008
Pardosa palustris	*Gryllus sigillatus*	6	6.752	Brose et al 2008
Philonthus fuscipennis	*Drosophila hydei* (Imago, flightless)	9	16.840	Brose et al 2008
Philonthus fuscipennis	*Lucilia caesar* (Larvae)	5	0.815	Brose et al 2008
Philonthus fuscipennis	*Tenebrio molitor* (Larvae)	6	0.349	unpublished
Pirata spec.	*Heteromurus nitidus*	13	159.641	Brose et al 2008
Pirata spec.	*Gryllus sigillatus*	12	6.205	Brose et al 2008
Pisaura mirabilis	*Heteromurus nitidus*	6	665.476	Brose et al 2008
Pisaura mirabilis	*Gryllus sigillatus*	7	22.062	Brose et al 2008
Poecilus cupreus	*Drosophila hydei* (Imago, flightless)	6	59.932	unpublished
Poecilus cupreus	*Lucilia caesar* (Larvae)	1	3.569	unpublished
Poecilus cupreus	*Tenebrio molitor* (Larvae)	1	1.593	unpublished
Poecilus versicolor	*Drosophila hydei* (Imago, flightless)	70	41.450	Brose et al 2008; unpublished
Poecilus versicolor	*Lucilia caesar* (Larvae)	53	2.375	Brose et al 2008; unpublished
Poecilus versicolor	*Tenebrio molitor* (Larvae)	17	1.027	unpublished
Pterostichus burmeisteri	*Drosophila hydei* (Imago, flightless)	21	72.815	unpublished
Pterostichus burmeisteri	*Lucilia caesar* (Larvae)	3	4.338	unpublished
Pterostichus burmeisteri	*Tenebrio molitor* (Larvae)	3	1.870	unpublished
Pterostichus melanarius	*Drosophila hydei* (Imago, flightless)	36	102.725	Vucic-Pestic et al 2010
Pterostichus melanarius	*Lucilia caesar* (Larvae)	38	6.660	Brose et al 2008, unpublished
Pterostichus melanarius	*Alphitobius diaperinus* (Larvae)	36	6.794	Vucic-Pestic et al 2010
Pterostichus oblongopunctatus	*Drosophila hydei* (Imago, flightless)	45	46.651	Vucic-Pestic et al 2010
Pterostichus oblongopunctatus	*Lucilia caesar* (Larvae)	37	2.753	Brose et al 2008, unpublished
Pterostichus oblongopunctatus	*Tenebrio molitor* (Larvae)	11	1.151	unpublished
Pterostichus oblongopunctatus	*Alphitobius diaperinus* (Larvae)	29	2.994	Vucic-Pestic et al 2010
Salticus scenicus	*Heteromurus nitidus*	5	20.667	Brose et al 2008
Salticus scenicus	*Gryllus sigillatus*	2	3.326	Brose et al 2008
Staphylinidae	*Drosophila hydei* (Imago, flightless)	3	20.916	unpublished
Trochosa terricola	*Heteromurus nitidus*	218	254.102	Vucic-Pestic et al 2010; Rall et al 2011
Trochosa terricola	*Gryllus sigillatus*	6	20.258	Brose et al 2008
Trochosa terricola	*Drosophila hydei* (Imago, flightless)	164	28.090	Vucic-Pestic et al 2010; Rall et al 2011

Functional response models and parameters

Overview of functional response models and the parameter estimates that were (1) derived from the model fittings to our feeding rate data and (2) afterwards used in the population dynamic simulations. All subsequent equations refer to the basic Holling type-II functional response where the per capita consumption rate of the consumer, F, depends on the density of the resource, N

$$F = \frac{aN}{1 + ahN} \quad \text{(S1)},$$

with handling time h and capture rate a.

Traditional Type-II functional response:

The basic assumption of allometric scaling according to the metabolic theory of Brown and colleagues (2004) is that metabolic rates scale with a ¾ power law with the body mass of the organism (Yodzis and Innes (1992) refer to Peters (1983) as reference for their use of the ¾-exponent). As the consumer has to balance its metabolic rate the maximum possible feeding rate, F_{max}, should also scale with a ¾ power law:

$$F_{max} = F_{max0}\, m_c^{0.75} \quad \text{(S2)},$$

where m_c is the body mass of the consumer and F_{max0} is a constant. As F_{max} is the inverse of handling time (Koen-Alonso 2007) it can be written as

$$h = \frac{1}{F_{max}} = \frac{1}{F_{max0}\, m_c^{0.75}} = h_0\, m_c^{-0.75} \quad \text{(S3)}.$$

Furthermore, following general allometric and energetic assumptions for the null model, the handling time for the resource should scale positively and linearly with its mass, m_r (e.g., a double amount of food needs double the time to be consumed). Therefore, equ. (S3) can be extended to

$$h = h_0\, m_r^1\, m_c^{-0.75} \quad \text{(S4)}.$$

To parametrise the entire functional response model according to Yodzis and Innes (1992) we have taken the following relationship, where B_0 is the half saturation density:

$$B_0 = \frac{1}{a\,h} \qquad \text{(S5)}.$$

As Yodzis and Innes (1992) used constant half saturation densities independent of species' body masses it follows that the body-mass dependency of the capture rate a has to be inverse of that of the handling time h that they can cancel each other out:

$$a = a_0\, m_r^{-1}\, m_c^{0.75} \qquad \text{(S6)}.$$

Table 2.3.C: Traditional type-II functional response parameter estimates

parameter	estimate	s.e.	t	p	
a_0	1.684×10^{-10}	7.127×10^{12}	23.62	$< 2 \times 10^{-16}$	***
h_0	4.106×10^{5}	1.791×10^{4}	22.93	$< 2 \times 10^{-16}$	***

Hump-shaped functional response:

$$a = a_0\, m_r^{\beta_r} \frac{m_c}{m_r}\, e^{\varepsilon \frac{m_c}{m_r}} \qquad \text{(S7)},$$

$$h = h_0\, m_c^{c_c}\, m_r^{c_r} \qquad \text{(S8)}.$$

Table 2.3.D: Hump-shaped type-II functional response parameter estimates

parameter	estimate	s.e.	t	p	
a_0	5.449×10^{-8}	1.511×10^{-8}	3.61	0.000316	***
h_0	5.511×10^{4}	1.500×10^{4}	3.67	0.000244	***
ε	-1.889×10^{-3}	1.101×10^{-4}	-17.16	$< 2 \times 10^{-16}$	***
β_r	4.463×10^{-1}	3.746×10^{-2}	11.91	$< 2 \times 10^{-16}$	***
c_r	6.498×10^{-1}	3.265×10^{-2}	19.90	$< 2 \times 10^{-16}$	***
c_c	-3.156×10^{-1}	5.481×10^{-2}	-5.76	9.45×10^{-9}	***

Generalised allometric functional response:

$$a = b\, N^q \qquad \text{(S9)}$$

$$h = h_0\, m_r^{c_r}\, m_c^{c_c} \qquad \text{(S10)},$$

$$b = b_0\, m_r^{\beta_r} \frac{m_c}{m_r}\, e^{\varepsilon \frac{m_c}{m_r}} \qquad \text{(S11)},$$

$$q = \frac{q_{max}\, R^2}{q_0^2 + R^2} \qquad \text{(S12)}.$$

Table 2.3.E: Generalised allometric functional-response parameter estimates

parameter	estimate	s.e.	t	p	
b_0	1.212×10^{-8}	2.912×10^{-9}	4.16	3.25×10^{-5}	***
β_r	-6.747×10^{-3}	3.420×10^{-2}	-0.20	0.844	
ε	-1.891×10^{-2}	7.897×10^{-4}	-23.95	$< 2 \times 10^{-16}$	***
q_{max}	3.422	1.444×10^{-1}	23.71	$< 2 \times 10^{-16}$	***
q_0	9.965×10^{2}	1.983×10^{1}	50.25	$< 2 \times 10^{-16}$	***
h_0	3.596×10^{4}	6.986×10^{3}	5.15	2.83×10^{-7}	***
c_r	5.440×10^{-1}	2.187×10^{-2}	24.87	$< 2 \times 10^{-16}$	***
c_c	-2.738×10^{-1}	2.128×10^{-2}	-12.87	$< 2 \times 10^{-16}$	***

AIC's

Table 2.3.F: AIC-values for model evaluation

Model	AIC	Δ AIC	df
Traditional type-II functional response	39069.89	1703.74	3
Hump-shaped functional response	38011.67	645.52	7
Generalised allometric functional response	37366.14	0	9

Model simulation

We performed a simulation of population dynamics to assess the persistence domain of a predator in dependence on its own and its prey's body mass. Persistence of the predator was assumed, if the minima of its population density did not fall below 10^{-30} individuals. The changes in population density per second of prey, N_r, and predator, N_c, were defined as ordinary differential equations (Yodzis & Innes 1992; Otto *et al.* 2007).

$$\frac{dN_r}{dt} = rN_r\left(\frac{1-N_r}{K}\right) - FN_c \quad , \tag{C1}$$

$$\frac{dN_c}{dt} = eFN_c - xN_r \quad , \tag{C2}$$

Here, the prey followed a logistic growth. The growth rate ($ind_r\ m^{-2}\ s^{-1}$),

$$r = 8.703\times10^{-8} m_r^{-0.25} \quad , \tag{C3}$$

scaled negatively with body mass, based on empirical parameters for growth rate (Savage *et al.* 2004) adjusted to a temperature of 15 °C. The carrying capacity ($ind_r\ m^{-2}$),

$$K = 1 m_r^{-0.72} \quad , \tag{C4}$$

was defined to be one $ind_r\ m^{-2}$ for a prey of one gram body mass, scaling negatively with body mass with an empirically derived exponent (Meehan 2006). The prey was consumed by each predator individual with the dynamic feeding rate, F (equation C1), which is a function of prey density. Here, the three allometric functional-response models, which were parametrised to the experimentally observed feeding rates (see Functional response models and parameters above for the respective parameter estimates), are substituted. This yielded three different, model-specific predictions of the persistence domain. The predator's density increased each second with the density lost from the prey population, FN_c, times the assimilation efficiency,

$$e = 0.85\frac{m_r}{m_c} \quad , \tag{C5}$$

which comprises the increase in predator density from one consumed prey individual, using the assimilation factor 0.85 for biomass conversion of predators (Peters 1983). The predator's energetic demands are modelled as

$$x = 4.083 \times 10^{-8} m_c^{-0.31} \quad , \qquad \text{(C6)}$$

scaled negatively with body mass, based on empirical parameters for metabolic rate (Ehnes, Rall, & Brose 2011) adjusted to a temperature of 15 °C.

The differential equations were implemented in C++ and solved by using procedures from the GNU Scientific Library [4th order Runge-Kutta-Fehlberg method with 5th order error estimate; (Galassi 2009)]. The population density at the start of the simulation was set to $N_c = 0.01$ (ind$_c$ m^{-2}) and $N_r = 1$ (ind$_r$ m^{-2}). Predator and prey body masses, $\log_{10} m_c$ and $\log_{10} m_r$, were varied systematically in the ranges from −3.5 to 0.5 for predators and −4 to 0 for prey with a step width of 0.005. Population dynamics ran over 10^{10} seconds into a steady state. Only the minimal values of the predator population density were saved (Figs. 2.3.3 A,B,C).

Subsequently we extracted all predator-prey pairs within the body mass range covered by the simulation from the Biodiversity Exploratories meta-food-web (see Methods: Soil food-web below). For each predator-prey pair and each of the three models substituted for *F*, a link was predicted, if the minimum of the model simulation at this point was larger than 10^{-30}. This allowed calculation of the percentage of those empirical links which lie within the area of persistence predicted by the model.

Methods: Soil food-web

The meta-web used to extract predator-prey pairs for this study was assembled based on 48 sub-webs sampled in the spring of 2008 at 48 forest sites in three geographical regions within the research project Biodiversity Exploratories in Germany (Fischer *et al.* 2010). Soil samples were taken with soil cores and heat extraction following the methods described in (Macfadyen 1961) and (Kempson, Lloyd, & Ghelardi 1963). Subsequently, species were determined and the length of each individual was measured. The body masses were calculated using mass length regressions based on an unpublished database on soil invertebrate body-sizes from Roswitha Ehnes (Technische Universität Darmstadt).

We used available data on stable isotope signatures [e.g., (Oelbermann & Scheu 2010), B. Klarner, Georg-August Universität Göttingen, unpublished data] to sort all species into trophic groups (e.g., fungivores, herbivores). Furthermore, the predators were assigned to different trophic levels. Feeding interactions were then estimated by literature research to detect possible links (Moulder & Reichle 1972; Dunger 2008; McLaughlin, Jonsson, & Emmerson 2010) but also those that could be excluded according to other sources [e.g., oribatid mites are not eaten by macrofauna generalist predators (Peschel *et al.* 2006)]. If available data was not sufficient to establish whether there was a link or not, we used molecular gut content analysis to verify the interaction (B. Eitzinger, Georg-August Universität Göttingen, unpublished data). Some of the species were divided into size classes because they differed significantly in mean body sizes between different plots. For the model test in Figure 2.3.3 we extracted every predator-prey pair together with the corresponding body-mass information resulting in an interaction matrix with 8 446 links.

2.4. The allometry of prey preferences

a) Summary

The distribution of weak and strong non-linear feeding interactions (i.e., functional responses) across the links of complex food webs is critically important for their stability. While empirical advances have unravelled constraints on single-prey functional responses, their validity in the context of complex food webs where most predators have multiple prey remains uncertain. In this study, we present conceptual evidence for the invalidity of strictly density-dependent consumption as the null model in multi-prey experiments. Instead, we employ two-prey functional responses parametrised with allometric scaling relationships of the functional response parameters that were derived from a previous single-prey functional response study as novel null models. Our experiments included predators of different sizes from two taxonomical groups (wolf spiders and ground beetles) simultaneously preying on one small and one large prey species. We define compliance with the null model predictions (based on two independent single-prey functional responses) as passive preferences or passive switching, and deviations from the null model as active preferences or active switching. Our results indicate active and passive preferences for the larger prey by predators that are at least twice the size of the larger prey. Moreover, our approach revealed that active preferences increased significantly with the predator-prey body-mass ratio. Together with prior allometric scaling relationships of functional response parameters, this preference allometry may allow estimating the distribution of functional response parameters across the myriads of interactions in natural ecosystems.

b) Introduction

Despite decades of ecological research on species interactions, the vast complexity of most natural communities still challenges our understanding of population and community stability (McCann 2000; Montoya *et al.* 2006). The plethora of predator-prey interactions in complex food webs contrast negative complexity-stability relationships in random interaction networks (May 1972). As a general null expectation, they suggest that complex natural food webs should be unstable unless they possess non-random structures. Interestingly, theoretical research has demonstrated how the distribution of weak and strong interactions across complex food webs determines the community-level stability (Neutel *et al.* 2002; Montoya *et al.* 2006; Brose 2008; Gross *et al.* 2009; Berlow *et al.* 2009). In particular, research on body-mass constraints on interaction strengths and adaptive foraging has provided major mechanistic insights into these patterns (Cohen *et al.* 1993; Kondoh 2003; Emmerson & Raffaelli 2004; Brose *et al.* 2006b; a; Otto *et al.* 2007; Rall *et al.* 2008; Ings *et al.* 2009; Brose 2010; Riede *et al.* 2011). Empirically, however, progress has been hampered by the lack of approaches that can be generalised across the myriads of interactions in complex food webs. Allometric functional responses predicting consumption rates by predator and prey body masses [(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Brose *et al.* 2008); chapters 2.1. and 2.2.] and environmental temperature (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011) provide a critically important first step towards such generality. However, they focus on single-prey interactions, while ignoring the complexity of natural communities, where predators are exposed to multiple prey. Here, we present an approach to generalize allometric interaction strengths from single-prey to multi-prey experiments.

One of the standard measures of interaction strength in food webs (Berlow *et al.* 2004) is provided by predator-prey functional responses (Solomon 1949; Holling 1959a) describing the per capita consumption rate of a predator, F, depending on prey density, N:

$$F = \frac{aN}{1 + aT_h N} \qquad (2.4.1),$$

where N is prey abundance, T_h is the handling time needed to kill, ingest and digest an individual of the prey and a is the attack rate [hereafter: "capture rate" sensu (Koen-Alonso 2007)]. This type II functional response with a constant capture rate can be modified to account for capture rates that vary with prey

density, $a = bN^q$ (Real 1977; Williams & Martinez 2004b; Rall *et al.* 2008), which yields type III functional responses:

$$F = \frac{bN^{q+1}}{1 + bT_h N^{q+1}} \qquad (2.4.2),$$

where b is a capture coefficient (sometimes also referred to as search coefficient), and q is a scaling exponent that converts hyperbolic type II ($q = 0$) into sigmoid type III ($q > 0$) functional responses [see Fig. 2.4.1a; note that some authors refer to intermediate or modified type II functional responses for values $0 < q < 1$; e.g., (Williams & Martinez 2004b)]. The Hill exponent, h, used in some prior studies (e.g., (Real 1977)) is equivalent to q ($h = q + 1$). Interestingly, the plethora of functional response studies concentrates on single-predator – single-prey studies (see (Hansen, Bjornsen, & Hansen 1997; Jeschke *et al.* 2004; Englund *et al.* 2011) for an overview). Nevertheless, the question remains if these findings hold when predator and prey are embedded in the complex network of a natural community, where most predators have multiple prey.

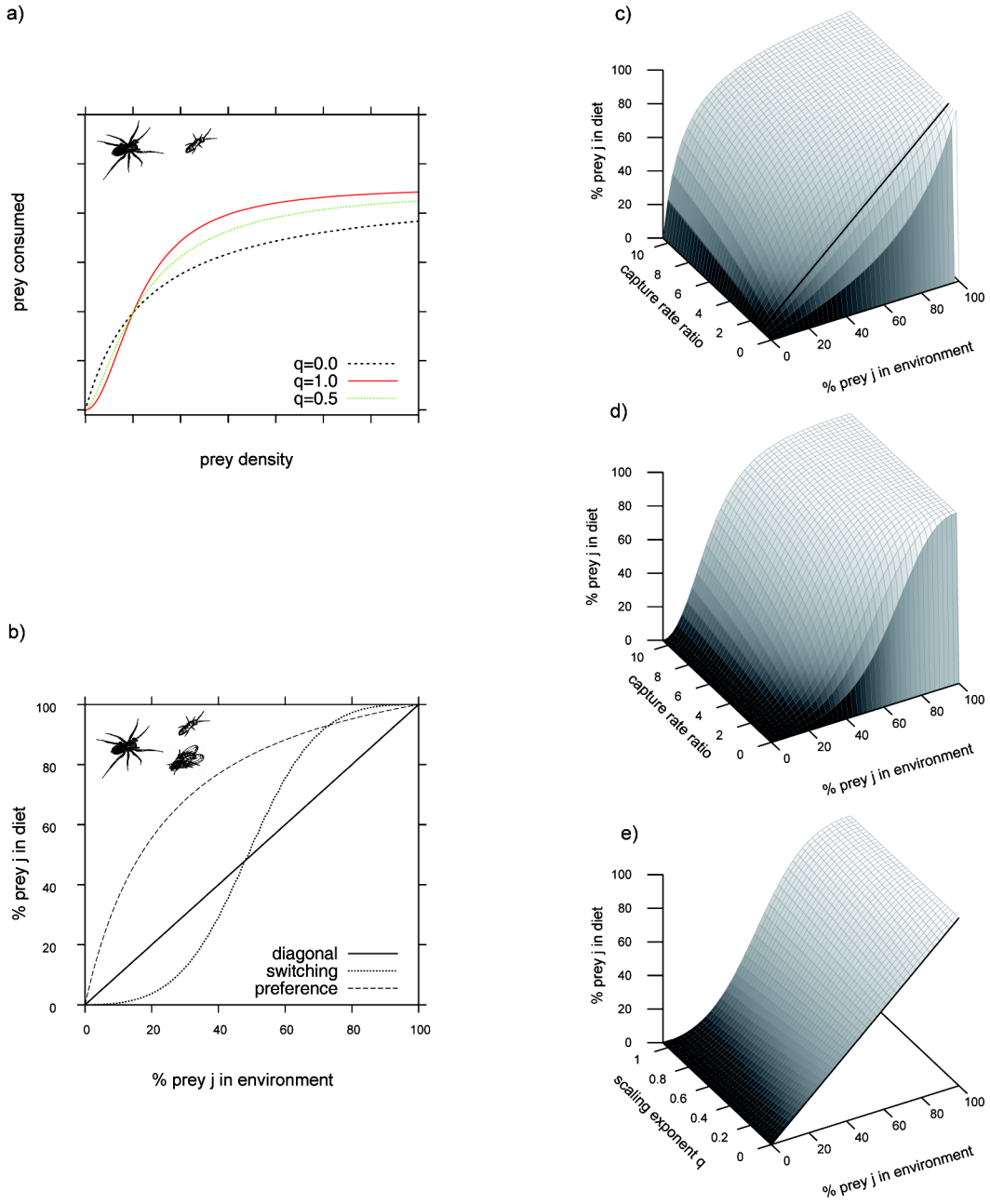
To overcome this deficit we increased the complexity of the experimental setting by the comparisons of single-prey functional responses from chapter 2.1. with two-prey experiments under identical experimental conditions, an experimental design rarely found in the literature (but see (Colton 1987; Elliott 2004, 2006) for examples). Traditionally, however, most two-prey experiments that were designed as to investigate preference and switching behaviour have simplified this approach by (1) skipping the single-prey functional response experiments, and (2) varying the relative densities of both prey while keeping a constant total prey density (Murdoch 1969; Landry 1981; Hughes & Croy 1993; Sundell *et al.* 2003). These approaches are illustrated in Figure 1. The diagonal representing strictly density dependent consumption has often been used as the null model (Fig. 2.4.1b, solid line). Hence, deviations from it were interpreted as preference for one prey (Fig. 2.4.1b, dashed line) or prey switching (Fig. 2.4.1b, dotted line) as an indicator of adaptive foraging behaviour (Murdoch 1969; Murdoch *et al.* 1975; Landry 1981; Hughes & Croy 1993; Carnicer, Abrams, & Jordano 2008). Historically, the quest for switching and adaptive foraging behaviour has been fuelled by its stabilising effect on population dynamics (Murdoch & Oaten 1975; Oaten & Murdoch 1975a; Williams & Martinez 2004b; Rall *et al.* 2008). One crucially important question remaining is whether strict density dependence (i.e., the diagonal in Fig. 2.4.1b) is a reasonable null model and consistent with predictions of the two single-prey functional responses. The functional response concept can be extended to a two-prey version:

Figure 2.4.1: Conceptual illustrations of **(a)** type II and type III (single-prey) functional responses and the implications of variance in the scaling exponent q as well as consequences for *absolute* prey consumption and (b-e) preferences and switching in two-prey (here: j and k) experiments: (**b)** "Traditional" preference plot with *relative* consumption depending on relative density of prey j: Consumption is strictly density-dependent (the diagonal solid line), or exhibits preferences for prey j (upper, long-dashed line) or switching behaviour (sigmoid, dotted line). c-e) Novel null model based on two-prey species functional responses (Equation 3) with varying capture rate ratios (b_{ij}/b_{ik} with $0.01 < b_{ij} < 10$ and $b_{ik} = 1$) for the two prey species in **(c)** type II ($q_{ij} = q_{ik} = 0$) and **(d)** type III functional responses ($q_{ij} = q_{ik} = 1$). **(e)** Gradual conversion of type II to type III functional responses when both prey are consumed with the same capture rate ($b_{ij} = b_{ik} = 1$). Constant handling time is used in figures c-e ($T_{hij} = T_{hik} = 0.1$). Note that the diagonal of strictly density-dependent consumption as the traditional null model (panel b) only emerges if both prey are consumed with exactly the same type II functional response (solid black lines in figures c and e)

$$F_{ij} = \frac{b_{ij} N_j^{(q_{ij}+1)}}{1 + b_{ij} T_{hij} N_j^{(q_{ij}+1)} + b_{ik} T_{hik} N_k^{(q_{ik}+1)}} \qquad (2.4.3),$$

where the per capita consumption of predator i on prey j depends also on the interaction between predator i and prey k (Murdoch 1973; Murdoch & Oaten 1975; Koen-Alonso 2007). Inserting the parameters of the two single-prey functional responses (i-j and i-k) in this model yields predictions of relative consumption within a two-prey experiment (Fig. 2.4.1c-e). If both single-prey functional responses are of type II (i.e. $q_{ij} = q_{ik} = 0$), variance in the capture rates b_{ij} and b_{ik} (while $T_{hij} = T_{hik}$) can result in substantial variation in the predicted relative feeding rates of the two-prey experiment (Fig. 2.4.1c). Strictly density dependent consumption (i.e. the highlighted diagonal solid line in Fig. 2.4.1c) only emerges if b_{ij} and b_{ik} are identical. If both single-prey functional responses are of type III, sigmoid feeding curves are predicted for all combinations of capture rates, and the diagonal indicating density-dependent consumption does not occur on the predicted consumption plane (Fig. 2.4.1d). Thus, even if the two single-prey functional responses are characterised by the same handling and capture parameters (i.e., $b_{ij} = b_{ik}$ and $T_{hij} = T_{hik}$), strictly density dependent consumption in the two-prey experiment is only predicted for pure type II functional responses ($q_{ij} = q_{ik} = 0$, Fig. 2.4.1e).

Together, these conceptual patterns have shown that strictly density-dependent consumption (i.e., the diagonal line in Fig. 2.4.1b) can only be used as the null model in two-prey experiments in the unlikely situation that both prey species are consumed with exactly the same type II functional response. In all other cases, deviation from strictly density-dependent consumption can simply be a consequence of inherent characteristics of the predator-prey relationship (e.g. physiological or morphological constraints like limitations of the digestive system or gape-size limitation) manifested in different capture rates (and/or handling



times as well as scaling exponents). Thus, the separation of active switching (i.e. switching behaviour deviating from single-prey based predictions) from passive switching (i.e. switching behaviour complying with single-prey based predictions) has been proposed (Gentleman *et al.* 2003). We propose to further expand this concept by also separating active preferences (i.e., preference or avoidance behaviour deviating from single-prey based predictions) from passive preferences

(i.e., preference or avoidance behaviour complying with single-prey based predictions).

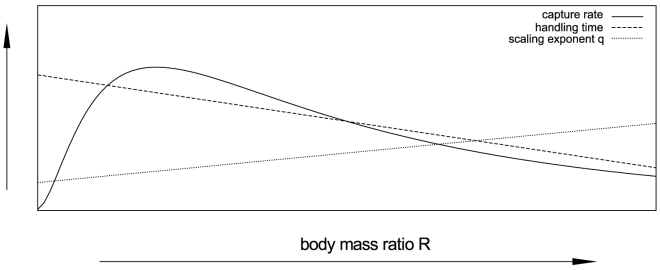


Figure 2.4.2: Conceptual graphic showing allometric relationships in the single-prey functional response parameters capture rate *a*, handling time *h* and the scaling exponent *q* as revealed in chapters 2.1. and 2.3.

Ecology has profited tremendously from replacing linear with non-linear null models in biodiversity research [i.e., neutral theory (Hubbell 2001) or mid-domain models of biodiversity (Colwell & Lees 2000)]. In the same vein, we propose that the wide-spread linear null model of strictly density dependent consumption is lacking realism and should be replaced by non-linear multi-prey functional responses. At the cost of increased complexity, they introduce more ecological plausibility and provide a deeper mechanistic understanding of predator-prey interactions. Subsequently, we will illustrate the use and potential of these non-linear null models in consumption experiments with terrestrial predators.

In the tradition of metabolic scaling models (Peters 1983; Ehnes *et al.* 2011), several studies dealing with a wide range of organisms revealed how capture rates (sometimes referred to as capture coefficients e.g., (Skalski & Gilliam 2001)) and handling time depend on body masses. In these relationships, handling times increase with increasing prey mass but decrease with increasing predator mass (Thompson 1975; Hassell *et al.* 1976; Spitze 1985; Vonesh & Bolker 2005), while capture rates follow hump shaped relationships with predator-prey body-mass ratios [(Spitze 1985; Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005), see also chapters 2.1. and 2.2.]. Regarding the allometry of the scaling factor *q* we are not aware of any other study but the one by Vucic-Pestic and colleagues (chapter 2.1.).

Here, we used allometric single-prey functional response models from chapter 2.1. to predict the per capita feeding rates in two-prey experiments (Eq. 2.4.3) using parameters from chapter 2.1. to predict our two-prey experiments (see Methods section below for details). We hypothesised that allometric functional response parameters should predict the consumption rates in the two-prey experiments thus resulting in “passive preferences” or “passive

switching". Alternatively, we aimed at explaining deviations from the multi-prey functional responses, equivalent to "active preferences" or "active switching", by predator-prey body mass ratios.

c) Materials and Methods

Allometric single-prey functional responses

In chapter 2.1. we addressed systematic effects of predator and prey body masses on the functional response parameters handling time, T_h, capture rate, a, and the scaling exponent q in experiments with 13 predator species comprising ground beetles and wolf spiders. The allometric dependence of handling time was estimated as:

$$\log_{10} T_h = p \log_{10} M_P + n \log_{10} M_N + \log_{10} T_{h(0)} \qquad (2.4.4),$$

with M_P as predator mass, M_N as prey mass, and p, n, $T_{h(0)}$ as constants. Furthermore, a hump-shaped relation for the capture coefficient b was defined as:

$$\log_{10}\left(b_{(R)}+1\right) = A \frac{\exp\left(\varepsilon\left(\Phi - \log_{10}\left(R+1\right)\right)\right)}{1+\exp\left(\beta\varepsilon\left(\Phi - \log_{10}\left(R+1\right)\right)\right)} \qquad (2.4.5),$$

where A is a constant, Φ represents the body mass ratio at which 50% of the maximum capture coefficient is reached, ε is the rate of change in search with mass controlling the steepness of the curve, R is the body-mass ratio (M_P/M_N) and ß determines the asymmetry of the curve. The handling time decreased with predator mass and increased with prey mass (see chapter 2.1.). Furthermore, capture rates followed hump-shaped relationships with predator–prey body-mass ratios. The scaling exponent, q, was low for predator-prey pairs with low body mass ratios (i.e. spiders - springtails and beetles – *fruit flies*) and high for the ones with high body mass ratios (i.e. spiders – *fruit flies* and beetles – *lesser mealworm* larvae) (see chapter 2.1.). These parameter combinations yield hump shaped functional responses as presented in Figure 2.4.3a-d.

Preference experiments

The experimental setting of our study followed the methods of previous studies (Brose *et al.* 2008; Rall *et al.* 2010; Vucic-Pestic *et al.* 2011): The predator individuals were kept separate in plastic jars dispersed with water and were

deprived of food for at least 48 hours before the start of the experiments. The experiments were performed in Perspex® arenas (20x20x10 cm) covered with lids. The lids contained gauze-covered holes to allow for gas exchange. The arena floor was covered with moist plaster of Paris (200 g dry weight) to provide constant moisture during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.35 g dry weight) that was first dried for several days at 40°C to exclude other animals and then re–moisturised prior to the experiments. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to adjust to the arenas. The experiment was run for 24 hours with a day/night rhythm of 12/12 h dark/light and temperature of 15°C in temperature cabinets. Initial and final prey densities were used to calculate the number of prey individuals eaten. Control experiments without predators showed that prey mortality or escape was negligible.

The predator species represent a subset of a those deployed within the previous study on allometric functional responses (see chapter 2.1.) including three wolf spiders (Aranea: Lycosidae) and three ground beetles (Coleoptera: Carabidae) that were weighed individually before the experiments. Consistent with predator body masses from chapter 2.1., they were spanning a relatively wide range of body masses (Table 2.4.1). All animals in the experiments were either sampled by pitfall trapping outside protected areas around Darmstadt, Germany, or they were reared in laboratory cultures. Pitfall trapping was conducted at agricultural field sites with acknowledgment of land owners. None of the animal species involved are threatened of extinction nor is any one of them under protection.

Due to logistic constraints, it was impossible within the present study to test the two-species allometric functional response model with all of the predator-prey combinations that were analysed in chapter 2.1.. Nevertheless we used the same prey species and prey sizes as in chapter 2.1.: in the experiments with spiders the springtails *Heteromurus nitidus* (0.15 mg) and flightless fruit flies *Drosophila hydei* (1.42 mg) were deployed as small and large prey, respectively (hereafter: *Heteromurus* and *Drosophila*). Meanwhile in the experiments with ground beetles the flightless *Drosophila* was the small prey while larvae of the lesser mealworm *Alphitobius diaperinus* (23.26 mg) were available as large prey (hereafter: *Alphitobius*).

Following the procedures of prior studies (Brose *et al.* 2008; Rall *et al.* 2010), the overall prey densities in the preference experiments were kept constant at 30 individuals while systematically varying the relative prey densities between one

small and 29 large prey individuals and 29 small and one large prey individual. Due to logistic constraints the experiments were carried out with ten and eight levels of relative density for wolf spiders and ground beetles, respectively. Each density level was replicated between six and eight times resulting in a total number of 352 experimental units. In the unique case of the ground beetle *Anchomenus dorsalis* (predicted capture rate on large prey *Alphitobius b*=0) 58 replicates were discarded before statistical analyses because total consumption in these replicates was zero and thus calculating relative consumption was impossible. After the experimental duration of 24 hours, individual predators were removed and weighed and remaining individual prey were counted. Prey individuals that were killed and partly consumed were counted as consumed. Individual predator weights before and after the experiments were then used to calculate individual average body weight.

Models and statistical analyses

Figure 2.4.3 shows the single-prey functional response curves (derived from chapter 2.1.) of the twelve predator-prey combinations that we tested within the present study: Fig. 2.4.3a shows the results for wolf spiders preying on the large prey species *Drosophila* and Fig. 2.4.3b shows the results for the small prey species *Heteromurus*. Fig. 2.4.3d and 2.4.3e show the single-prey functional response curves for three ground beetles preying on *Alphitobius* and *Drosophila* as large and small prey, respectively. The curves are plotted within a three-dimensional plot with body mass ratio R as y-axis to visualise the realised range of predator-prey body mass ratios. Additionally, we present the planes of the single-prey allometric functional response models that were derived from the previous study and subsequently applied to parametrise the two-prey functional response model predictions (see Table 2.4.1 for parameter values from chapter 2.1.). The results of the model predictions for the two prey allometric functional response model are shown in figures 2.4.3c and 2.4.3f for wolf spiders and ground beetles, respectively, where the body mass ratio R on the y-axis represents the ratio between predator and the larger prey.

Note that both, the single-prey as well as the two-prey functional response model, assume a constant prey density throughout the experiment and the prey depletion following consumption was corrected by integrating over time and prey density [(Royama 1971; Rogers 1972); see chapter 2.1. for more details]. While single-prey functional responses allow analytical solutions, referred to as Rogers' random predator equation (Rogers 1972), experiments with two prey species

required numerical integration. Therefore we inserted Equations (2.4.4) and (2.4.5) into Equation (2.4.3) and integrated the resulting equation over time ($dN_i / dt = -F_{ijk}$) to predict how feeding rates should behave in a two-prey predation experiment using the additional R package "deSolve" applying a Runge-Kutta 4th order integration algorithm in R 2.11.1 (R Development Core Team 2010; Soetaert, Petzoldt, & Setzer 2010). Eqs. (2.4.4) and (2.4.5) were parametrised according to empirical predator masses as well as parameter values from chapter 2.1.; see also Table 2.4.1) and two separate simulation settings were established for spiders and beetles, respectively (according to the different scaling exponents). Consistent with the experiments, the overall prey density (i.e., individuals of large prey plus individuals of small prey per arena) in the numerical simulations was set to 30 individuals while the experimental duration of 24 hours was split into 240 time steps (i.e., one time step = 6 minutes). The empirical results from the two-prey experiments were then compared to the numerically simulated prediction and checked for significant deviations by student's t-tests. Non-significant residuals (i.e., deviation of consumption from simulated two-prey functional response prediction) were interpreted as support for our initial hypothesis that allometric functional responses predict the consumption rates in two-prey experiments. Subsequently, we analysed the residuals by an ANCOVA using R 2.11.1 (R Development Core Team 2010) to distinguish between effects of (1) the body-mass ratio between the predator and the large prey, (2) predator group (beetle or spider) and (3) level of relative initial density of the large prey.

Table 2.4.1: Parameters of the allometric two-prey functional response model as the null model for the preference experiment (Figs. 3 and 4): N = number of replicates; M_P = average predator mass [mg]; R = average predator-prey body-mass ratio; q = capture exponent; * parameters taken from chapter 2.1..

	N	M_P	R (predator:large prey)	q(large prey) *	q(small prey)*
spiders	207			0.17	0.52
Trochosa terricola juvenile	69	2.766	1.95		
Pardosa lugubris	70	28.895	20.35		
Trochosa terricola adult	68	78.874	55.55		
beetles	145			0.02	0.89
Anchomenus dorsalis	48	12.108	0.52		
Calathus fuscipes	49	65.712	2.83		
Harpalus rufipes	48	120.561	5.18		
Parameters applied in Eqs. (2.4.4) and (2.4.5) *	P= -0.94; n= 0.83; $Th_{(0)}$= 0.35; A= 3.69; ε = 0.48; Φ = 0.45; β = 47.13				

d) Results

Numerical simulations of preference predictions

The results of the numerical simulations for expected passive preference patterns depending on predator body masses are shown in Fig. 2.4.3e and f for spiders and beetles, respectively. Despite differences in both the scaling exponents q and the prey masses, the transition from predicted passive avoidance to passive preference for the larger prey occurs at a "tipping point" with body mass ratios of roughly two (i.e., predator is twice as large as the larger prey) for spiders and beetles. This phenomenon was recorded in both plots by an abrupt shift from zero consumption along all relative prey densities to strong preference for the larger prey within a relatively short range along the body-mass ratio axis. Interestingly, we did not find any indication of predicted passive switching (Fig. 2.4.3e and f).

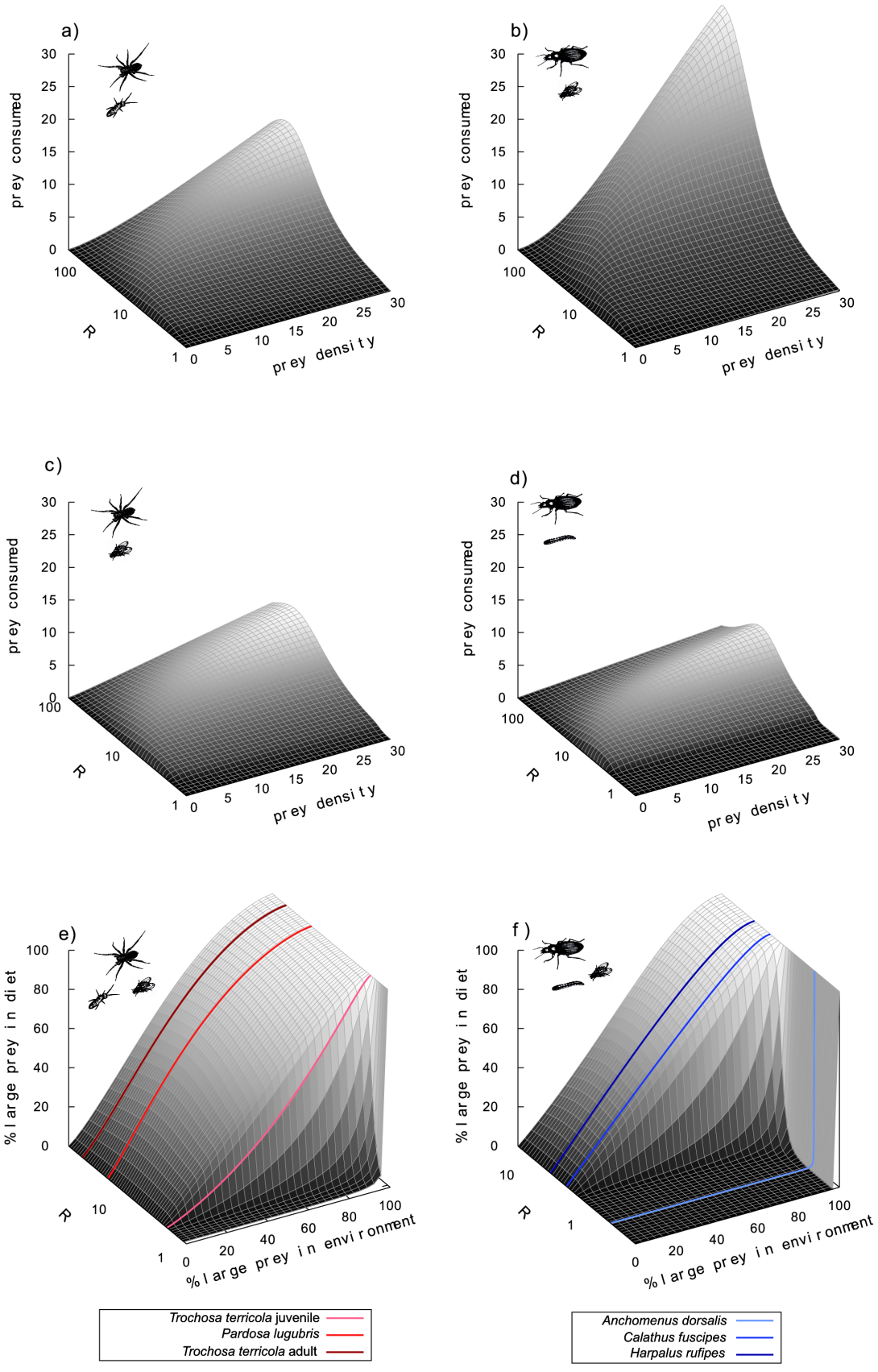
Two-prey experiments

We tested the predictions of the allometric two-prey functional model for six predators: three spiders (predicted orange preference lines in Fig. 2.4.3e) and three beetles (predicted blue preference lines in Fig. 2.4.3f). The two-prey functional response models predicted passive preferences for the smaller prey in the experiments with the smallest spider (red line in Fig. 2.4.4a) and the smallest beetle (blue line in Fig. 2.4.4b), whereas all larger predators were expected to exhibit passive preference for the larger prey (Fig. 2.4.4c-f). Interestingly, the

novel null model based on allometric two-prey functional responses (coloured lines in Fig. 2.4.4) differs in all experiments from the traditional null model of strictly density-dependent consumption (diagonals in Fig. 2.4.4).

Subsequently, we compared the empirical consumption rates to the two-prey functional response null model (coloured lines in Fig. 2.4.4). In four of the six two-prey experiments, we found substantial and significant deviations of the empirical consumption rates from model predictions (Fig. 2.4.4). This indicates active preferences for the larger prey by the wolf spiders *P. lugubris* (Fig. 2.4.4c) and *T. terricola* (adult) (Fig. 2.4.4e) and the ground beetles *A. dorsalis* (Fig. 2.4.4b) and *H. rufipes* (Fig. 2.4.4f). Interestingly, the two predators that fulfil the criteria for passive preference are those with body mass ratios close to the "tipping point" of roughly two (*T. terricola* juvenile, Fig 2.4.4a and *C. fuscipes*, Fig. 2.4.4d). The active preferences for the larger prey are evenly distributed across relative prey densities for *P. lugubris*, *T. terricola* and *H. rufipes* (Fig. 2.4.4c, e, f), whereas the smallest beetle, *A. dorsalis*, exhibited active preference for the larger prey only at the highest initial relative density of the larger prey (relative initial density > 80%, Fig. 2.4.4b).

Figure 2.4.3: Single prey functional responses as a function of predator-prey body mass ratios from a previous study (chapter 2.1.) for the following predator-prey combinations: **(a)** wolf spiders – *Drosophila*, **(b)** ground beetles – *Alphitobius*, **(c)** wolf- spiders – *Heteromurus* and, **(d)** ground beetles – *Drosophila*. Parameters applied for these models are given in Table 1. Combining of the single-prey functional responses for one large and one small prey allowed calculating predictions of the allometric functional response models for the two-prey preference experiment with **(e)** spiders (body-mass range from 1 to 200 mg) with *Drosophila* as large prey and *Heteromurus* as small prey, and **(f)** beetles (body-mass range from 1 to 600 mg) with *Drosophila* as small and *Alphitobius* larvae as large prey. The coloured lines indicate the six species (i.e., body size classes) that were tested empirically in this study (see Fig. 2.4.4). Note the difference between *absolute* consumption in plots (a-d) while (e) and (f) show *relative* consumption on the x- and z-axes. Note that for the two-prey plots (e and f) the predator-prey body-mass ratio (R) on the y-axes relates to the ratio between the predator and its larger prey.


a)
b)
c)
d)
e)
f)
prey consumed
prey density
R
% large prey in diet
% large prey in environment
Trochosa terricola juvenile
Pardosa lugubris
Trochosa terricola adult
Anchomenus dorsalis
Calathus fuscipes
Harpalus rufipes

A full factorial ANCOVA of the residuals revealed a highly significant three-way interaction term between predator group, square of relative initial prey density and the predator-prey body-mass ratio ($F_{7,344} = 26.41$, $p < 0.001$, $r^2 = 0.35$). For subsequent more detailed ANCOVAs addressing this three-way interaction term, we separated the data sets into two predator groups. The ANCOVA of the beetles revealed a highly significant two-way interaction term between the square of relative initial prey density and predator-prey body mass ratio ($F_{3,141} = 33.22$, $p < 0.001$, $r^2 = 0.41$). In the spider dataset, we removed the interaction term and found that predator-prey body mass ratio as well as the initial densities were significantly affecting the results ($F_{2,204} = 16.76$, $p < 0.001$, $r^2 = 0.14$). Interestingly, the residuals increased with predator-prey body-mass ratios for both predator groups (Fig. 2.4.5a and b), though the slope was much steeper for beetles (slope = 46.58 ± 8.64 (s.e.), Fig. 2.4.5b) than for spiders (slope = 5.67 ± 2.59 (s.e.), Fig. 2.4.5a). However, spiders and beetles responded differently in

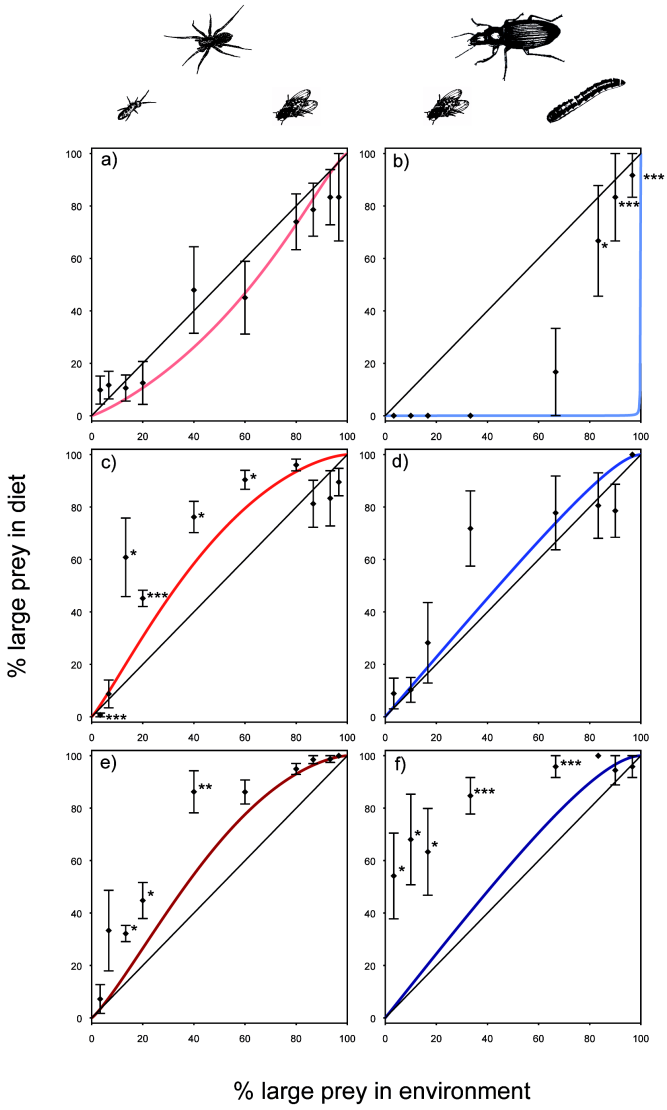


Figure 2.4.4: Two-prey consumption experiments for (a,c,e) spiders with *Drosophila* as large prey and *Heteromurus* as small prey, and (b,d,f) beetles with *Drosophila* as small and *Alphitobius* larvae as large prey. Solid black lines indicate traditional null model of strictly density-dependent consumption, coloured lines show predictions of the allometric two-prey functional response model (see Fig. 3). Black diamonds show mean consumption in two-prey experiments, vertical bars indicate standard errors. T-test significance levels are indicated as: * <0.05, ** <0.01 and *** <0.001. Panels show the results for **(a)** *Trochosa terricola* juvenile, **(b)** *Anchomenus dorsalis*, **(c)** *Pardosa lugubris*, **(d)** *Calathus fucscipes,* **(e)** *Trochosa terricola* adult and **(f)** *Harpalus rufipes*.

their active preferences to the relative initial density of the large prey: while spiders showed a weak negative relationship (slope = –0.002 ± 0.0004 (s.e.), Fig. 2.4.5c), the relationship for the beetles was positive (slope = 0.005 ± 0.0008 (s.e.), Fig. 2.4.5d).

e) Discussion

In this study, we addressed the question whether laboratory functional response experiments combining predators with single prey species can predict the outcome of experiments with two prey species. Conceptually, we demonstrated that strictly density dependent consumption only emerges from multi-prey functional responses as the null expectation if both prey species are consumed with exactly the same type II functional response. Employing empirical allometric two-prey functional-response models as a novel null model in our study yielded consumption rates that varied substantially from strict density dependence without implying any active foraging choices by the predators. We refer to these deviations as passive preferences. While the general pattern of passive preferences for larger and smaller prey with predator-prey body-mass ratios higher and lower than two, respectively, was correctly predicted by the two-prey functional responses, the majority of the predators exhibited additional active preferences for the larger prey. This consistent deviation from the null model suggests a general allometry of preferences.

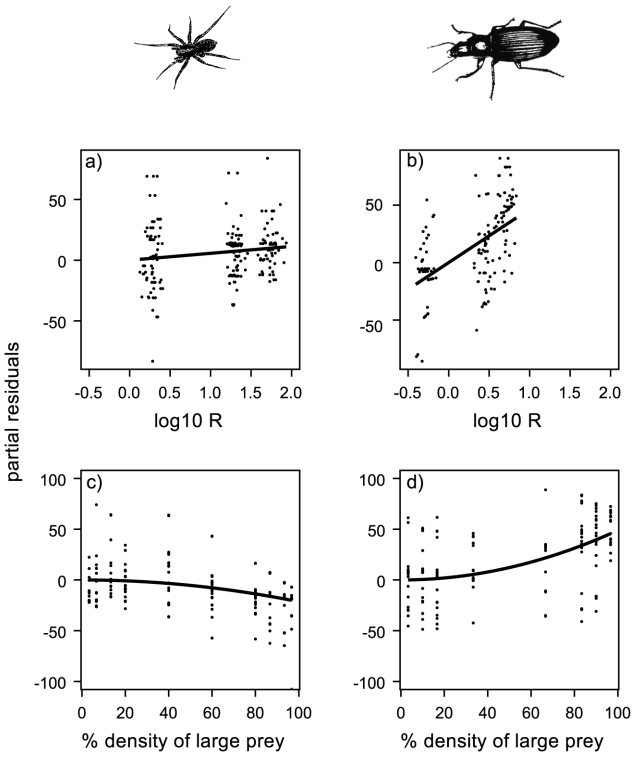


Figure 2.4.5: Active preferences (partial residuals) for the larger prey of **(a, c)** spiders and **(b, d)** beetles depending on the body-mass ratio between the predator and the larger prey (a, b) and the square of relative initial densities (c, d). Parameters: a) slope = 5.674, (s.e. ± 2.594) intercept = 7.699 (s.e. ± 4.734); b) slope = -0.002 (s.e. ± 0.0004) intercept = 7.699 (s.e. ± 4.734); c) slope = 46.575 (s.e. ± 8.644), intercept = 5.227 (s.e. ± 4.402); d) slope = 0.005 (s.e. ± 0.0008) intercept = 5.227 (s.e. ± 4.402).

Simple null model

We illustrated the consequences of the popular fallacy of using strictly density-dependent consumption as the null model in two-prey experiments on preferences or switching behaviour. While some studies have correctly employed multi-prey functional responses as the null model (e.g., (Colton 1987; Elliott 2004, 2006)), most prior studies avoided the labour-intensive development of all single-prey functional responses and used strictly density-dependent consumption as a more simple null model (e.g., (Murdoch 1969; Murdoch *et al.* 1975; Landry 1981; Hughes & Croy 1993)). Our conceptual examples (Fig. 2.4.1c-e) illustrate that this simple null model is only acceptable if both prey are consumed with exactly the same type-II functional response. As functional response parameters vary dramatically across different prey species (e.g., (Houde & Schekter 1980; Hansen *et al.* 1997; Mckee *et al.* 1997; Galarowicz & Wahl 2005; Pervez & Omkar 2005; Smout & Lindstrøm 2007), see also chapters 2.1. and 2.2.), we suggest that the simple null model of strictly density-dependent consumption will rarely apply. Unfortunately, this violation of the underlying assumptions invalidates the conclusions on preferences or switching drawn by many prior studies (e.g., (Murdoch 1969; Landry 1981; Hughes & Croy 1993; Sundell *et al.* 2003; Carnicer *et al.* 2008)).

Allometric null model

We demonstrated how multi-prey functional-responses parametrised by single-prey experiments can be used as an alternative more adequate null model in two-prey experiments (Fig. 2.4.3e and f). To avoid the labour-intensive study of all single-prey functional responses, we have proposed allometric functional response models as an alternative. These models represent systematic relationships between functional response parameters such as handling time and capture rate (see chapters 2.1. - 2.3.). The body masses of the species in two-prey experiments can parametrise these relationships that are subsequently entered in two-prey functional responses. Together, allometric relationships and two-prey functional responses provide novel null models predicting expected predator consumption rates if the co-occurrence of the two prey species does not influence the interactions. Obviously, allometric scaling relationships might provide inaccurate estimates of functional-response parameters. In this study, the twelve individual single-prey functional responses necessary to parametrise the six two-prey models were available from a prior study (chapter 2.1.). However, predictions based on these single-prey functional responses were entirely

consistent with those of the allometric functional response models. We have thus decided to base the presentation of the null model in the present study on the allometric functional-response models, because they will allow a more wide-spread application in other studies where the single-prey functional responses are not necessarily available. In our study, the steep rise from zero consumption for low body mass ratios (here: ratio between predator and large prey: $R \leq 2$) regardless of the relative prey densities is consistent for both predator groups and may be due to the steep rise in capture rates with body-mass ratios on the left hand side of this hump. One has to bear in mind that this well documented hump-shaped relationship arises from different constraints on foraging rates at the two different sides of the hump (Brose 2010).

In this study, variation in the body-mass ratio was only included at the level of the individual predators that were weighed for every single treatment. At the prey level, however, we worked with fixed average sizes for the three prey species resulting in fixed body-mass ratios between large and small prey for all treatments, because data on prey of other sizes were not available from the previous study (chapter 2.1.). Therefore, future studies on allometric functional responses (*i.e.*, single-prey *and* multi-prey studies) should include more variation in prey body size to extend the allometric functional response concept. Nevertheless, the allometric concept provides a general framework for parametrising interaction strengths within complex food webs.

Passive and active preferences

Moreover, the allometric two-prey functional responses take inherent characteristics of predator-prey relationships into account and thus allow deeper mechanistic understanding of predator choices. Most importantly, the novel null model allows to clearly separate between passive and active preferences. We define “passive preference” as a deviation from strictly density-dependent consumption driven by morphological, physiological and behavioural (evolutionary) adaptations that constitute a specific predator-prey interaction in both the simplified (i.e., one prey) as well as a more complex (i.e., multiple prey) environment. In contrast, “active preference” implies significant differences among simplified and more complex environments induced by short-term behavioural changes (e.g., different rate of attacks upon encounter if an alternative prey is present). Our analyses show passive as well as active preferences, and they allow separating the body-mass constraints leading to passive preferences from predator choices yielding systematic active preferences

for the larger prey by most predators. We refer to this entirely novel and systematic pattern as the "allometry of preferences".

Passive and active switching

Interestingly, our systematic exploration of the novel null model demonstrated the potential for passive switching if the passive preferences of the predator switch between prey depending on their relative density. This phenomenon is generally expected if both single-prey functional responses are of type III. Although the spiders in our experiments exhibited a type III functional response on both prey, the consumption rates predicted for the two-prey experiments did not include any passive switching. This apparent contradiction is explained by the numerical integration procedure to account for prey depletion during the experiments: The low prey densities in the numerical simulation of the two-prey model prevented passive switching. However, incorrectly using the simple multi-prey functional response without accounting for prey depletion yielded predictions of slight passive switching among prey. Generally, we would expect passive switching only if both single-prey functional responses were more strongly sigmoid (closer to a "true" type III functional response with q=1) and thus both scaling exponents were considerably higher than 0.2 (Williams & Martinez 2004b).

To our knowledge, laboratory studies that found switching predators mostly introduced this effect by the design of the study through providing distinct sub-habitats [e.g., (Murdoch *et al.* 1975; Elliott 2004)]. While the predators in these studies were "forced" to change their foraging mode according to the distribution of the different prey items, our study was designed to provide a uniform habitat. Nevertheless, the exploration of our two-prey null model suggests that type III functional responses can cause passive switching, which is counter-intuitive compared to conventional wisdom in population ecology (Gentleman *et al.* 2003; Koen-Alonso 2007). While strongly stabilising effects of adaptive foraging in theoretical studies (Valdovinos *et al.* 2010) have triggered a quest for empirical documentation of switching [e.g., (Carnicer *et al.* 2008)], we caution that adaptive foraging requires active variation in prey preferences, which cannot be deduced from sigmoid consumption rates crossing the diagonal line of strictly density-dependent consumption. Our results stress the need to adopt more sophisticated null models such as the allometrically parametrised two-prey functional responses to provide empirical support for adaptive foraging.

Experiment

In our experiments, four of the six predators showed active preferences for their larger prey indicated by significant deviations from the null model predictions. Meanwhile we found passive preferences close to a density dependent consumption for the small spiders (juvenile *T. terricola*) as well as for the intermediately sized beetle (*C. fuscipes*). Interestingly, all predator-prey interactions with body-mass ratios larger than two (adult *T. terricola*, *P. lugubris* and *H. rufipes*) exhibited strong active preferences for the larger prey. This entirely novel preference allometry is supported by statistically significant increases in active preferences with predator-prey body-mass ratios. Moreover, the relative densities of the two prey species exhibited additional effects on preferences, which were skewed in opposite directions for beetles and spiders. Despite this opposite effect of relative prey densities and differences in the strength of the increase in preference with body-mass ratios between beetles and spiders, this general pattern allows more accurate generalisations of functional responses across the myriads of interactions in complex food webs. Our analyses may also explain a more general pattern that larger carnivorous mammals focus on large prey, whereas small carnivorous mammals focus on small prey as revealed in a large meta-study (Carbone *et al.* 1999).

Caveats

We found a different pattern of active preferences for the larger prey by the smallest beetle *A. dorsalis*: despite a low body-mass ratio (0.52) we found active preferences for the larger prey at the highest relative prey densities. While a previous single-prey functional response experiment indicated that the large individuals from this prey species are too big to overwhelm and ingest for the small beetle *A. dorsalis*, we found in the present experiment that single events of this feeding interaction occasionally occurred (though the results are somehow skewed as we had to discard 58 replicates for zero consumption). One possible explanation is that we could not control the body masses of every prey individual, and *A. dorsalis* overwhelmed particularly those prey individuals smaller than the average mass of 23 mg. Additionally, *A. dorsalis* was not able to ingest the whole prey individual in the experimental time of 24 hours. Moreover, *A. dorsalis* is relatively inefficient at catching the smaller prey, flightless *Drosophila*: For instance, the capture rates of similarly sized spiders on *Drosophila* is two orders of magnitude higher ($b = 36.3$ for *A. dorsalis* compared to $b = 1\,500$ for *P. lugubris*; chapter 2.1.). Together, these specific constraints on *A. dorsalis* may

explain how stochastic effects have caused active preferences at the highest relative prey densities. In principle, however, this example highlights that allometric models trade predictive power in specific cases for the sake of gaining generality across species. Interestingly, the concept of allometric functional responses is flexible to incorporate phylogenetic constraints (see chapter 2.2.) which allows tailoring accurate models for specific experiments.

f) Conclusions

Our conceptual approach demonstrated that the wide-spread use of the simple null model of strictly density-dependent consumption is impeding mechanistic advances. Instead, progress requires application of more sophisticated null models for two-prey experiments such as the allometric two-prey functional response. Our analyses revealed systematic patterns of active and passive preferences. In particular, the majority of predators actively preferred the large prey. If this finding of a systematic preference allometry generalises across additional predator groups and other ecosystem types, we anticipate that it may provide towards a general understanding of constraints on interaction strengths in natural communities. This may have substantial importance in creating the patterns of many weak and few strong interactions that stabilise natural food webs.

2.5. Habitat structure alters top-down control in litter communities

a) Summary

The question whether top-down or bottom-up forces dominate trophic relationships, energy flows and abundances within food webs has fuelled ecological research with a particular focus on soil and litter ecosystems for decades. Due to the fact that litter simultaneously provides habitat structure and the basal resource, disentangling direct trophic and indirect non-trophic effects on different trophic levels remains challenging. Here, we focussed on short term per capita interaction strengths of generalist predators (centipedes) on their detritivore prey (springtails) and addressed how the habitat structuring effects of the leaf litter modifiy this interaction. We performed a series of laboratory functional response experiments where four levels of habitat structure were realised by adding different amounts of beech leaf litter to the experimental arenas. We found that increasing the amount of leaf litter reduces the feeding rate of the predator. We interpreted this as a dilution effect of the augmented habitat-size provided by the increasing leaf litter surface available to the species. Dilution of the prey population decreases encounter rates, whereas the capture success is not affected. Interestingly, our results imply that top-down control by centipedes decreases with increasing resource supply for the detritivore prey (i.e., the leaf litter that simultaneously provides habitat structure). This non-trophic effect of the basal litter resource on the top predator thus prevents that bottom-up supply translates into top-down control of detritivore populations.

b) Introduction

Progress in food-web ecology is critically based upon information about bioenergetic flows of energy between consumer-resource pairs. These interaction strengths and their distributions across the myriads of links in natural food webs are vital for community structure, population dynamics, and ecosystem functioning [e.g., (McCann *et al.* 1998; Neutel *et al.* 2002; Otto *et al.* 2007; Neutel *et al.* 2007; Rall *et al.* 2008; Berlow *et al.* 2009; Binzer *et al.* 2011)]. One major question in the ecology of soil food webs therefore deals with the regulation of detritivore populations and whether they are controlled by bottom-up mechanisms (i.e. energy and nutrient supply) or top-down regulated by their multiple predators. Both hypotheses are supported by several studies: Bengtsson et al. (1997) found top-down control, whereas the results of Scheu and Schäfer (1998) and Ponsard et al. (2000) provided evidence for bottom-up control. Major progress in this field requires insights into consumer-resource interactions with a particular focus on the strength of such interactions (Scheu 2002). Due to the natural composition of soil-litter habitats with their porous, fractal structure and opacity, the direct observation of species interactions in the natural context is almost intractable. Indirect observation via gut or stomach content analysis which is a standard procedure in freshwater [e.g., (Elliott & Persson 1978; Woodward & Hildrew 2002a)] and marine systems [e.g., (Daan 1973; Aljetlawi *et al.* 2004; Smout & Lindstrøm 2007)] is hampered by the fact that a large fraction of soil predators rely on extra-intestinal digestion (Cohen 1995) and therefore deep understanding of predator-prey interaction strengths in these systems remains challenging. While different methods of tracking feeding links *qualitatively* were developed and improved over the past decades – particularly stable isotope analyses, molecular gut content analyses and fatty acid trophic markers (Post 2002; King *et al.* 2008; Ruess & Chamberlain 2010) – they have scant ability of tracking feeding interactions *quantitatively*. Therefore, we have to rely on laboratory experiments to determine *per capita* impacts of litter- and soil-dwelling predators on their prey.

One well-established model framework for analysing interaction strengths is the functional response (Holling 1959b; Berlow *et al.* 2004). It describes the density dependent *per capita* feeding rate, F_{ij}, of a predator j on a prey i (Holling 1959b; Real 1977):

$$F_{ij} = \frac{a_{ij} N_i^{q+1}}{1 + a_{ij} h_{ij} N_i^{q+1}} \qquad (2.5.1),$$

where F_{ij} [$n_i\, n_j^{-1}\, d^{-1}$] is the per capita feeding rate, N_i [$n_i\, m^{-2}$] is the prey density, h_{ij} [$n_j\, d\, n_i^{-1}$] is the handling time needed to kill, ingest and digest a resource individual, a_{ij} is the capture rate [$m^2\, d^{-1}\, n_j^{-1}$] and q is a scaling exponent converting the hyperbolic type II functional response ($q = 0$) to a sigmoid type III functional resonse [$q = 1$; (Real 1977; Rall *et al.* 2008); see also chapters 2.1. and 2.3.). Note that the capture rate (often also referred to as "attack rate" or more accurately "rate of successful attacks") is expressed on a movement or velocity scale (with either area or volume as reference parameter depending on the foraging mode of the predator and the ecosystem type where the predator-prey interaction takes place). It includes the rates of encounter and success of attacks (Gergs & Ratte 2009).

Jeschke et al. (2004) highlighted that the majority of functional response studies are carried out in the laboratory under controlled conditions, usually within a simplified experimental environment that is far from natural conditions. This problem has been addressed by functional response studies focussing on mechanisms that added complexity to experimental conditions such as varying numbers of predators [predator interference – e.g., (Kratina *et al.* 2009; Lang *et al.* 2012)], the number of prey species [alternative prey – e.g., (Colton 1987; Elliott 2004); see also chapter 2.4.] or even the additional presence of non-prey species (Kratina *et al.* 2007). Further lack of reality in laboratory studies is based on simplified environmental conditions that given within artificial arenas. There is only a limited number of studies focussing on the effects of habitat complexity on the functional response of terrestrial predators (Kaiser 1983; Munyaneza & Obrycki 1997; Pitt & Ritchie 2002; Hoddle 2003; Hohberg & Traunspurger 2005; Hauzy *et al.* 2010; Vucic-Pestic *et al.* 2010a). While some of these studies focussed on the fractal complexity of an artificially structured habitat (Kaiser 1983; Pitt & Ritchie 2002; Hoddle 2003) and others made qualitative comparisons of with-structure- versus non-structure-treatments (Hohberg & Traunspurger 2005; Vucic-Pestic *et al.* 2010a), to our knowledge there is only one study with a qualitative comparison between a simplified, unstructured laboratory setting and field conditions. This study indicated reduced capture rates of terrestrial

arthropod predators by a factor of roughly two under green house and field conditions compared to the experimental setting with controlled conditions in the laboratory experiment (Munyaneza & Obrycki 1997). Especially in leaf-litter systems, where pulses of incoming material and long-lasting decay of the litter yield a continuously changing amount and complexity of habitat structure, our understanding of ecosystem dynamics and functioning is challenged by the general lack of studies addressing how habitat structure modifies interaction strengths and top-down control of detritivores by predators.

In this study, we aimed at filling this gap by studying the effects of systematic variation in leaf litter density on the functional response of the centipede *Lithobius mutabilis* (Chilopoda: Lithobiidae) as an ubiquitous and frequent generalist predator of the leaf-litter system on its detritivore prey, the springtail *Heteromurus nitidus* (Collembola: Entomobryidae). Within the model framework of the functional response, we expected prey refuges of the additional habitat structure to cause a shift from type II to type III functional responses (Real 1977; Scheffer & De Boer 1995). Furthermore we anticipated that the capture rates depending on encounter rates and attack success should be much more affected by changes in the environment than the handling times that include the time the predator needs to subdue, ingest and digest its prey as well as resting or cleaning itself (Hassell 1978). In consequence, we hypothesised that the increase of the amount and the complexity of leaf litter should (1) provide additional prey refuges therefore resulting in more sigmoid type III functional responses, (2) decrease the capture rates, and (3) not affect the handling times.

c) Material and Methods

Functional response experiments

The basic experimental set-up follows prior functional-response experiments [(Brose *et al.* 2008; Vucic-Pestic *et al.* 2011); see also chapters 2.1. - 2.3.]. We studied the *per capita* feeding rates of the centipede *L. mutabilis* on the springtail *H. nitidus* at varying prey densities from one to 1 000 individuals of springtails per arena (corresponding to 25 to 25 000 individuals per m²) at four levels of habitat complexity (one, two, four and eight grams dry weight of beech litter; corresponding to 25, 50, 100 and 200 grams per m²). Single prey density levels were replicated three to five times resulting in a total number of 123 experimental units. The centipedes were sampled by hand from field sites in the Hainich-Dün National Park, Thuringia, Germany. Freshly fallen beech litter was

sampled at the same sites. The predator individuals were kept separate from each other in moistened plastic jars and were deprived of food for at least 48 hours before the start of the experiments. The experiments were performed in acrylic glass arenas (0.2x0.2x0.1 m) covered with lids with holes to allow gas exchange. The arena floor was covered with moist plaster of Paris (200 g dry weight) to provide constant moisture during the experiments. Beech litter for providing habitat structure in the arenas was first dried for several days at 40°C to eliminate other animals and then re–moisturised prior to the experiments. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to adjust to the arenas. The experiments were run for 24 hours with a day/night rhythm of 12/12 h dark/light and a constant temperature of 15°C in temperature cabinets. Initial and final prey densities were used to calculate the number of prey individuals eaten. Control experiments without predators showed that effects of prey mortality or escape were negligible. As previous studies have shown strong allometric effects on the functional responses of terrestrial invertebrate predators (see chapters 2.1. - 2.3.) we controlled predator and prey weight and kept it at a constant level (centipedes: 22.74 mg ± 0.77 standard error; springtails: 0.15 mg ± 0.004 s.e.).

Leaf area

Generally, leaf litter density is positively correlated with surface area available for the predator-prey interaction. Hence, expressing feeding and capture rates relative to the surface area of the experimental arenas might become arbitrary with increasing leaf litter density. In order to provide an alternative approach accounting for increases in surface area with increasing leaf litter density, we "corrected" the prey densities relative to the leaf surface area plus the arena area to get the "total foraging area": Therefore we measured the leaf surface area of a representative set of twelve samples of leaves (three replicates of one, two and four gram dry weight, respectively) that were used within the experiments. For each sample, we determined leaf surface area by optical scanning with a flatbed graphics scanner and subsequent analyses of the images with the software WinFOLIA, V 5.1a (REGENT INSTRUMENTS INC., Québec, CANADA). We fitted leaf area against leaf-litter dry weight using a linear model. Subsequently, three different spatial scenarios were compared in our functional response analyses: (1.) *uncorrected* area, i.e. 0.04 m² arena surface area in all leaf litter treatments, (2.) *one-side corrected* area with the one-sided leaf area plus arena surface area, and (3.) *two-side corrected* area with the two-sided leaf area plus arena surface area (see Table 2.5.1 for an example how prey densities were

corrected for differing habitat size according to these three scenarios).

Statistical analyses

To investigate the shape of the functional response, we fitted a polynomial logistic regression to the proportion of prey eaten (Juliano 2001). A continuously decreasing relationship indicates a type II functional response, whereas a hump shaped curve indicates a type III functional response (see Juliano (2001) for detailed methodology). We found continuously decreasing functions for all four density treatments (data not shown) and used type II functional response models for further analyses. Subsequently, we repeated all analyses with (1.) the *uncorrected* prey densities that were identical in the four leaf litter density treatments (expressed as predator and prey individuals per arena surface area) and with *corrected* prey densities differing between the treatments on the basis of a (2.) one-sided and a (3.) two-sided leaf area correction (expressed as individuals per arena surface area plus the single-sided and the two-sided leaf surface area, respectively; see Table 2.5.1 for the example with a prey density of one individual per arena).

As equation (2.5.1) assumes a constant prey density throughout the experimental time we used the integrated form of the functional response, also known as Rogers 'Random Predator Equation' (Royama 1971; Rogers 1972) to avoid violation of our statistical results:

$$N_e = N_0\left(1 - e^{(a_{ij}(N_e h_{ij} - PT))}\right) \qquad (2.5.2),$$

where N_e [$n_i\,m^{-2}$] is the density of prey i eaten during the experiment, P is predator j's density, T is the experimental time [d] and all other parameters are as in equation (2.5.1). We solved this recursive function of N_e with a non linear least squares method ("nls") using the additional package "emdbook" provided by Ben Bolker for the statistical software package R (Bolker 2008; R Development Core Team 2010). The resulting equation is

$$N_e = N_0 - \frac{W\left(a_{ij} h_{ij} e^{(-(PT - h_{ij} N_0))}\right)}{a_{ij} h_{ij}} \qquad (2.5.3),$$

where W is the Lambert W function (see Bolker (2008) and references therein for a detailed description). Furthermore, we analysed the effect of litter density on capture rates and handling times by inserting either exponential functions:

$$a_{ij} = a_0 e^{\varepsilon_a L} \qquad 2.5.4,$$

and

$$h_{ij} = h_0 e^{\varepsilon_h L} \qquad 2.5.5,$$

or power law functions

$$a_{ij} = a_0 L^{(b_a)} \qquad 2.5.6,$$

and

$$h_{ij} = h_0 L^{(b_h)} \qquad 2.5.7,$$

in Eq. (2.5.3), where a_0 and h_0 are constants, L is the amount of leaf litter, ε_a and ε_h determine the exponential increase or decrease of capture rates and handling times with leaf litter dry weight, while b_a and b_h are the scaling exponents of the power law functions. Additionally, functional response models with constant values a_0 and h_0 without leaf-litter dependence were also fitted to the data. We fitted all possible combinations of the three capture-rate models and three handling-time models (constant, exponential, power law) under each of the three spatial scenarios (uncorrected, one-side and two-side correction) to the data resulting in a total of 27 functional response models (see Table 2.5.2 for an overview) and ranked them according to their ΔAIC.

Table 2.5.1: Results of leaf area linear model fit and examples of deduced density correction factors for one individual per experimental replicate.

leaf litter weight [g]	one-sided leaf area [m²]	95% confidence interval	ind./arena (0.04 m²)	uncorrected densities [ind/m²]	one-sided leaf area corrected densities [ind/m²]	two-sided leaf area corrected densities [ind/m²]
1	0.0234	± 0.0020	1	25	15.7633	11.5105
2	0.0469	± 0.0040	1	25	11.5105	7.4764
4	0.0938	± 0.0080	1	25	7.4764	4.3954
8	0.1875	± 0.0161	1	25	4.3954	2.4095

d) Results

The mean leaf area (one-sided) increased from 0.023 m² (± 0.002 95 % confidence interval) in the treatment with one gram leaf litter to 0.188 m² (± 0.016 95 % c.i.) in the treatment with eight gram leaf litter (Table 2.5.1, Figure 2.5.1 a-d) following a linear model fit through the leaf areas of one, two and four gram dry-weight of leaf litter (n = 12, $R^2 = 0.984$, $p < 0.0001$). This increase in the surface area available for animal movement and interactions implies that the prey density (here exemplified for one springtail individual per arena) decreases from 25 ind/m² (only arena surface, not accounting for leaf surface) to ~16 ind/m² (one-sided correction) and ~12 ind/m² (two-sided correction) in the treatment with

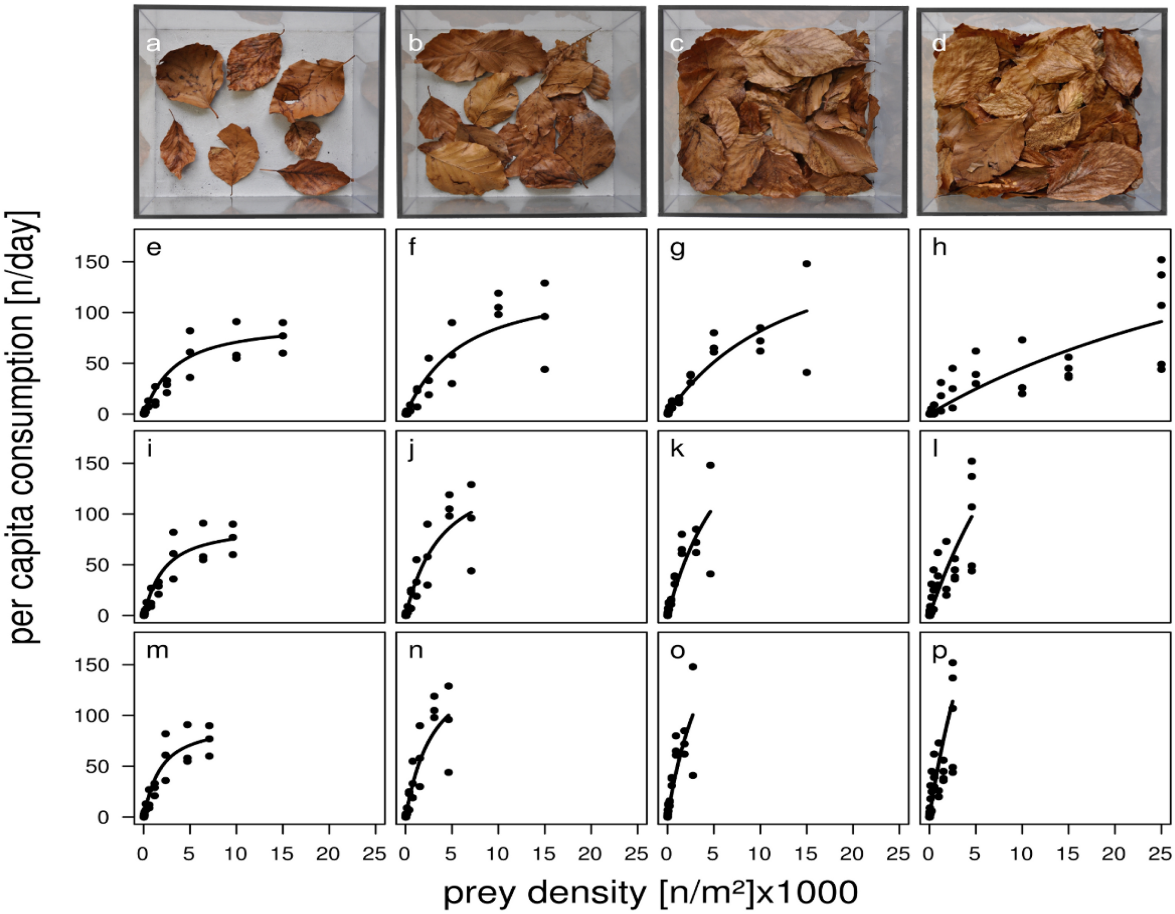


Figure 2.5.1: Pictures of the leaf litter within the experimental arenas (0.04m² ground area) of the four treatments with **(a)** one gram dry weight leaf litter, **(b)** two gram, **(c)** four gram and **(d)** eight gram. Beneath are the functional response curves according to the respective best-fitting model for the uncorrected (panels **e-h**), the one-side corrected (panels **i-l)** as well as the two-side corrected (panels **m-p**) densities. Parameter values are given in Table 2.5.3.

Table 2.5.2: Functional response model evaluation according to their ΔAIC with constant values, power law and exponential relationships in capture rates and handling times, respectively.

capture rate dependence	handling time dependence	df	ΔAIC
models without leaf area prey density correction			
exponential	power law	5	0.000
exponential	exponential	5	2.591
power law	power law	5	7.089
exponential	constant	4	7.747
power law	exponential	5	9.738
constant	exponential	4	12.248
power law	constant	4	14.068
constant	power law	4	16.011
constant	constant	3	19.162
models with one-sided leaf area prey density correction			
exponential	power law	5	0.000
exponential	exponential	5	2.616
power law	power law	5	2.773
constant	power law	4	3.258
power law	exponential	5	5.614
power law	constant	4	6.806
constant	exponential	4	13.620
exponential	constant	4	16.008
constant	constant	3	21.305
models with two-sided leaf area prey density correction			
constant	power law	4	0.000
exponential	power law	5	0.645
power law	power law	5	1.791
exponential	exponential	5	2.395
power law	exponential	5	4.251
power law	constant	4	4.945

one gram leaf litter or to ~4 ind/m² (one sided correction) and ~2 ind/m² (two sided correction) in the treatment with eight gram leaf litter (see Table 2.5.1 for details of this example and Fig. 2.5.1a-d for pictures of arenas with different amounts of leaf litter). While prey densities were the same across treatments in the scenario with uncorrected area (only accounting for the area of the arena; Fig. 2.5.1e-h: second row), the increases in leaf surface area with the amount of leaf litter resulted in a shift in prey densities from higher densities in treatments with one gram leaf litter (Fig. 2.5.1, left column) to lower densities (Fig. 2.5.1i-l: one-side correction; m-p: two-side correction).

We fitted polynomial logistic regressions to analyse the dependence of the proportion of prey consumed on uncorrected prey density. These analyses were independently replicated for all four treatments of leaf density. All four regressions exhibited non-significant higher order polynomials and continuously decreasing relationships (data not shown). Contrary to our first hypothesis, this does not provide any evidence for more sigmoid functional response curves (i.e., type III functional responses) with increasing habitat structure. In consequence, we used type II functional response models in all subsequent analyses (see Fig. 2.5.1 for fitted models). Consistent with our second initial hypothesis, capture rates showed decreasing exponential functions with increasing leaf litter density for the uncorrected and the one-side corrected prey densities, whereas functional-response models with a constant capture rate provided the best fit to the data under two-side correction (Table 2.5.2, Fig. 2.5.2a). Comparing the parameter values of the models with exponential relationships for capture rates, there is a

clear trend from a highly significant negative relationship for the uncorrected densities ($\varepsilon_a = -0.0103$, s.e. = 0.0014, $p < 0.0001$), a shallower slope with lower significance for the one-side correction ($\varepsilon_a = -0.0032$, s.e. = 0.0014, $p = 0.020$) to a non-significant (constant) relationship under the two-side correction ($\varepsilon_a = -0.0016$, s.e. = 0.0014, $p = 0.267$ in the second best model fitting; see Table 2.5.3 for parameter estimates for the best fitting models, respectively).

Surprisingly, in all three spatial scenarios (*uncorrected*, *one-side corrected* and *two-side corrected* densities) the best-fitting model with the lowest ΔAIC included power-law decreases in handling times with increasing leaf litter density (Tables 2.5.2 and 2.5.3; Fig. 2.5.2b). This contradicts our third initial hypothesis that handling time should not be affected by litter density. All of the functional response models with constant handling time yielded a much poorer fit to the data (Table 2.5.2) suggesting that our third hypothesis has to be rejected. The consequences of these litter dependencies in capture rates and handling times for

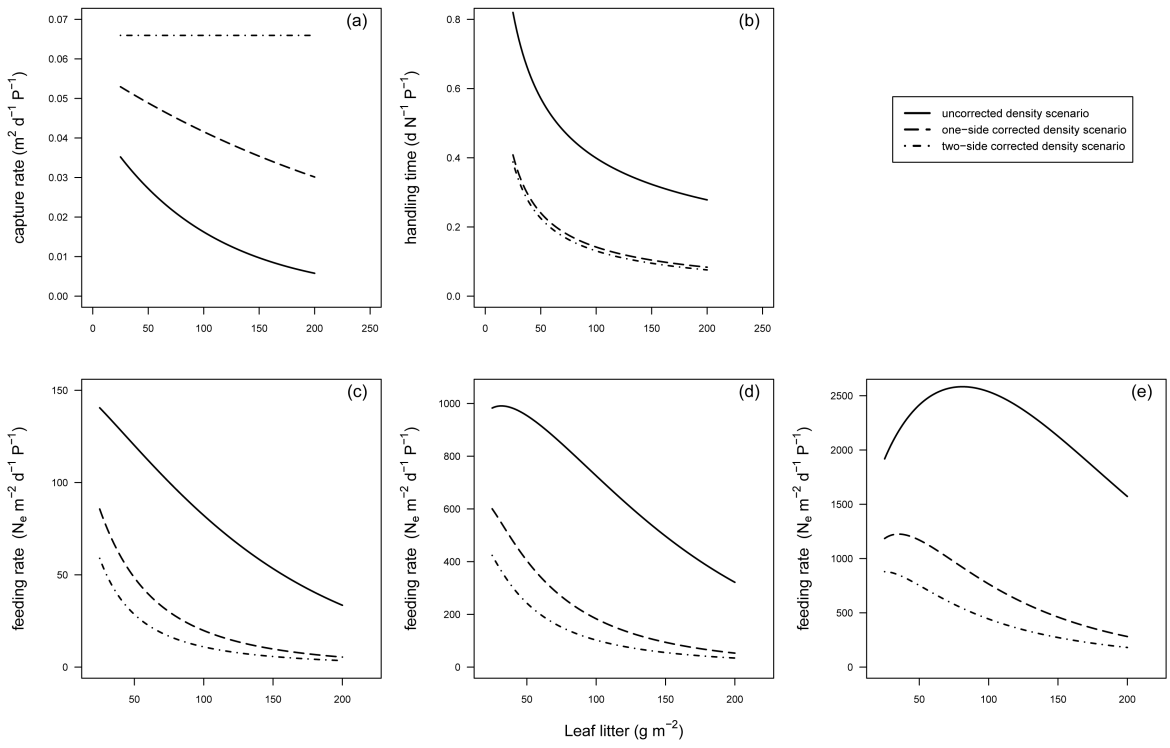


Figure 2.5.2: Relationship between leaf litter densities and **(a)** capture rates and **(b)** handling times. Curves are based on the best-fitting functional-response models with uncorrected (solid line), one-side corrected (dashed line) and two-side corrected prey densities (dash-dotted line). Panels c-e show the resulting relationships for leaf litter densities and feeding rates at ten **(c)**, 100 **(d)** and 600 **(e)** prey individuals per experimental arena.

the relationship between per capita feeding rates and the amount of leaf litter in the system are illustrated in Figure 2.5.2c-e for three exemplary prey densities: While the feeding rates decreased constantly with leaf litter density at low (Fig. 2.5.2c, ten springtails per arena) and intermediate prey densities (Fig. 2.5.2d, 100 springtails per arena) under all three spatial scenarios, we found a hump-shaped relationship at higher prey densities (Fig 2.5.2e, 600 springtails per arena) for the uncorrected and the one-side corrected scenario.

Table 2.5.3: Parameter estimates for best model fittings for uncorrected, one-side and two-side corrected densities, respectively. While handling times follow a power law relationship in all model approaches the capture rates depend on leaf litter density following an exponential relationship for uncorrected and one-side corrected densities. In the two-side correction approach we did not find leaf-litter dependence for the capture rate. Significance codes are given as: '***'< 0.001; '**' < 0.01; '*' < 0.05; '.' < 0.1

	parameter estimate	s.e.	t-value	p	
best fitting model without leaf area prey density correction					
a_0	0.0456	0.0118	3.877	< 0.001	***
ε_a	-0.0103	0.0014	-7.364	< 0.0001	***
h_0	0.0586	0.0354	1.653	0.101	
b_h	-0.5196	0.1675	-3.102	0.002	**
best fitting model with one-sided leaf area prey density correction					
a_0	0.0574	0.0109	5.289	< 0.0001	***
ε_a	-0.0032	0.0014	-2.361	0.020	*
h_0	0.1297	0.0730	1.777	0.078	.
b_h	-0.7618	0.1694	-4.497	< 0.0001	***
best fitting model with two-sided leaf area prey density correction					
a_0	0.0659	0.0086	7.705	< 0.0001	***
h_0	0.1340	0.0777	1.723	0.088	.
b_h	-0.7839	0.1810	-4.331	< 0.0001	***

e) Discussion

In this study, we tested how changing habitat structure in a leaf litter dominated ecosystem may influence predator-prey interactions by examining functional responses in a laboratory experiment. Contrary to our expectations, we have not found a switch from hyperbolic to sigmoid functional responses with increasingly complex habitat structure. Corroborating our expectations, we found a highly significant decrease in capture rates with increasing litter density except for our analyses correcting for increase in habitat area on both sides of the leaves (two-side correction) where capture rates remain constant. While we expected

handling times to be unaffected by leaf litter density, our analyses revealed decreasing handling times with increasing leaf litter densities. Eventually, the resulting feeding rates illustrate that top-down control on detritivores decreases with leaf litter density. In typical forest ecosystems with a dense litter layer, this non-trophic effect of habitat structure should thus release decomposers from top-down control.

As the functional responses showed a hyperbolic shape at each litter density, we suppose that the particular habitat structure realised by the beech leaf litter does not provide sufficient hiding refuges for the springtails within the experimental design employed. This may be due to the mobility and the particularly flattened shape of the centipede body allowing it to explore the interstices between the leaves in a similar fashion as its significantly smaller prey. Subsequent studies need to replicate our experiments for predator groups that differ in their ability to hunt within the interstices between the leaves to address the generality of our result.

Consistent with our initial hypothesis, the capture rates decreased with increasing litter density. We tested whether this effect is caused by (1) a dilution effect reducing encounter rates as increasing litter density yields a higher surface area of the leaves available for interactions or (2) decreases in the attack efficiency of the centipedes. We found that the significant decrease in capture rates with leaf litter densities is turned into a neutral relationship when accounting for increases in habitat size for springtails and centipedes with increasing surface area of the leaves. This finding is supported by the observation that centipedes and springtails move on the ground area of the experimental arena as well as on both sides of the leaves. In consequence, our results suggest that the attack efficiency of the centipedes does not change with litter density, whereas increasing habitat size reduces the encounter rates by diluting the prey population to lower densities. The constant capture rates in the analyses correcting for the two-sided increase in habitat size with leaf density show that the dilution effect is responsible for the negative relationship between capture rates and prey density in our experiment.

Surprisingly, we found significant decreases in handling time with litter density. As it is well known that centipedes are extremely sensitive to dry conditions [Lithobiids have been shown to prefer 90-100% relative humidity - (Albert 1983)], the treatments with higher litter density might have provided more humid conditions. These more suitable microclimatic conditions for the centipedes might be responsible for the decrease in handling time along the leaf

litter density gradient if physiological processes involved in ingestion become more efficient with humidity. However, other physiological processes driven by litter density might also contribute to our result.

As for any empirical study, some potential caveats need to be mentioned. The astute reader will have noticed that the functional-response models fitted under the spatially corrected scenarios did not reach a saturation, because correction of the densities compressed the prey density range. This is particularly important for the estimation of handling times in functional response model fitting. However, as our analyses have shown that the general patterns in leaf-litter dependency of the functional response parameters also apply for the well-saturated model fittings based on the uncorrected spatial scenario this should not affect our conclusions. Furthermore, we could have avoided unsaturated curves under the spatial correction scenarios by extending the range in prey densities beyond the maximum of 25 000 individuals per square meter. However, this would have by far exceeded the densities of natural springtail populations [biomasses of ~0.6 gram per m² corresponding to ~4 000 individuals per m²; calculations based on dry-weight data from Schaefer (1990) multiplied by water-fraction factor four from Peters (1983)]. In conclusion, we have decided to keep the springtail densities of our experiment within the range of natural densities while addressing the consequences of natural habitat structures on feeding rates, which avoids the fallacies imposed by oversimplified laboratory conditions (Munyaneza & Obrycki 1997; Vucic-Pestic *et al.* 2010a).

In soil food webs, springtails are amongst the most abundant taxonomic groups within the detritivore guild and therefore of critical importance for litter decomposition (Chen & Wise 1997). In a study with a focus on spider predation upon springtails, it has been shown that a reduction of springtails reduces litter decomposition rates (Lawrence & Wise 2000) indicating the importance of top-down regulating mechanisms in soil-litter systems. In this study, we present a novel mechanism how top-down control might be coupled to the dynamics of leaf litter fall with far reaching consequences for decomposition and population dynamics of detritivores and their predators. The non-trophic effect provided by habitat-altering leaf litter fall can be included in predator-prey functional responses by changing the densities of predators and prey.

Moreover, the capture rates and handling times are significantly affected by increasing leaf litter densities, but the consequences of these relationships are not straightforward: While decreasing handling times should lead to increasing feeding rates, decreasing capture rates should cause decreasing feeding rates.

Our analyses illustrate that feeding rates generally decrease with litter density, except for the combination of the highest springtail density with the lowest litter density. In consequence, the habitat modifications mediated by leaf litter fall and the subsequent decomposition processes might be responsible for regular shifts between bottom-up and top-down control regimes in some leaf-litter systems where phases of litter scarcity can occur due to fast decomposition processes (e.g., systems dominated by maple or alder leaf litter). Corresponding patterns in detritivore and predator population dynamics of mixed deciduous forests where predator abundances exceed detritivore abundances in the autumn have been documented in Ponsard et al. (2000). However, our results suggest that in litter-systems with slow decomposition rates (e.g., systems dominated by beech or oak leaf litter) the potential for top-down control of predators on decomposers should be weak. Our findings shed new light on the ongoing debate whether soil-litter systems are top-down or bottom-up regulated (de Ruiter *et al.* 1995; Polis & Strong 1996; Bengtsson *et al.* 1997; Scheu & Schaefer 1998). Interestingly, they illustrate that non-trophic effects of leaf litter drive the strength of predatory top-down control. Hence, understanding the importance of top-down and bottom-up control in soil ecosystems requires integrating trophic and non-trophic effects as it has recently been called for (Fontaine *et al.* 2011; Kéfi *et al.* 2012).

f) Conclusions

In this study we have shown how changes in habitat structure affect the predator-prey functional response in leaf litter systems by diluting predator and prey densities, which reduces their encounter rate. Hence, top-down control of decomposers might be restricted to ecosystems where leaf litter decomposition is fast enough to deplete habitat structure significantly within one vegetation period. In contrast, many typical temperate forest ecosystems are characterised by slow decomposition rates thus leading to thick litter layers with structured habitats. We have shown that this reduces top-down control by the dilution effect, whereas more complex indirect effects on capture efficiency could be ruled out. The spatial habitat structure of the litter layer thus determines the strength of predatory top-down control, which provides evidence that non-trophic interactions may govern ecosystem organisation.

3. General Discussion

To understand how populations, communities and ecosystems persist through time and space and, moreover, how they will react to anthropogenic stressors in the future, we need universally applicable tools that help us to gain general insights beyond specific, in-depth knowledge for every single interactor pair in nature. Recently, organism's body sizes and body masses have been suggested as a possible measure to tackle ecological questions in a more systematic way that may help to get general insights on the structure and functioning of ecosystems (Woodward *et al.* 2005; Ings *et al.* 2009; Brose 2010). Henceforth, this thesis was built on extensive, laboratory experiments on feeding rates of differently-sized terrestrial, generalist arthropod predators and their prey of different sizes. All experiments were evaluated and interpreted based on the functional response model framework [i.e., prey-density dependent feeding rates of predators; (Holling 1959a)] with predator and prey body sizes and habitat structure as additional, independent variables in the experimental setting. A key motivation for the work presented here might be described as the search for a specific form of the functional response (i.e., the traditional, sigmoid type-III response) that has long since been associated with stability-enhancing mechanisms in consumer-resource relationships (Murdoch & Oaten 1975; Oaten & Murdoch 1975a; Koen-Alonso 2007) and thus has been called the "Holy Grail of theoretical (population) ecology" (Bernstein 2000). However, empirical evidence suggested that hyperbolic, type-II responses prevailing in laboratory studies (Jeschke *et al.* 2004) tend to cause unstable predator-prey systems according to many theoretical studies [e.g., (Fussmann & Blasius 2005; Gentleman & Neuheimer 2008)]. The question arose whether the complexity in nature begets types of interactions that are inherently stable and that ecologists tend to overlook in many experimental settings. This is particularly challenging as ecosystems are composed of a bewildering diversity of species in contrast to the empirical evidence of unstable interaction strength (i.e., type-II responses) and theoretical instability of complex networks (May 1972). It is in the light of 40 years of this "diversity-stability debate" (McCann 2000) where this thesis becomes most meaningful and where the reader shall judge its scientific core messages. The key findings of this thesis include:

1. Large predator-prey body-size ratios cause sigmoid response curves and capture rates follow hump-shaped relations with predator-prey body-size ratios.

2. Body size is a better explanatory variable for variance in feeding rates of generalist predators than taxonomical differences.

3. The traditional distinction between type-II and type-III functional responses should be questioned, at least. A more realistic view driven by biological mechanisms comprises that predators feed on their differently sized prey according to an allometrically-constrained continuum between hyperbolic and sigmoid curves. The test of the modelling approach entailing this continuum showed outstanding accordance with the empirical predator-prey pairs from a totally independent database.

4. The predictive potential of the allometrically-parametrised functional-response models from simplified experiments (i.e., one prey species per experimental unit) for more complex settings (i.e., two different sized prey per treatment) seems limited. However, my approach showed that it is conceptually important to distinguish between passive and active feeding choices. Moreover, residual analyses showed that the larger the predator is in relation to its prey, the more accentuated becomes the active preference for larger prey.

5. Contrasting previous considerations about prey refuge effects, habitat structure does not create sigmoid responses *per se*. However, in the case of the predators from litter-dominated soil-habitats that I used in this thesis, I was able to show how reduced feeding rates under increased habitat complexity are achieved mechanistically. That is by a dilution effect of additional litter that increases the area that is available for foraging of predator and prey.

Taking these findings altogether and transferring them from laboratory with its simplified and standardised conditions to the real world, I propose the following consequences on predator-prey relationships in natural food webs: Basically, generalist predators should follow the optimality approach and take large prey whenever and wherever available – until a threshold where overcoming larger prey becomes intractable – resulting in the well documented hump-shaped patterns of capture rates. Moreover, my experiments and subsequent analyses have shown, that larger prey is "easier" to catch at low prey densities exemplified at hyperbolic response curves for large prey versus sigmoid response curves for smaller prey. The further interpretation of these findings should implicitly take natural abundance-size relationships into account as they are important for the interpretation of these results and their implementation in the field. The empirical pattern of many small and few large organisms is an intriguing fact that has been recognized and described several times starting

with Eltons' “pyramid of numbers” (Elton 1927) and later on formed the base of the size spectrum approach with its far-reaching implications for the aquatic sciences (Brooks & Dodson 1965; Sheldon *et al.* 1972). This pattern of many small and few large organisms has also been documented in soil communities (Meehan 2006; Mulder *et al.* 2009). Therefore I argue that the combination of preferences for large prey and the general mass-abundance patterns causes expression of many weak and few strong feeding links. This property had been shown to be one of the crucial factors for the stability of natural food webs (McCann *et al.* 1998; Neutel *et al.* 2002). I anticipate sigmoid response curves to be an important, though not exclusive, driver for the dominance of the weak-links. This idea is supported by the fact that potentially strong links as exemplified by many laboratory studies turn out to be weak(er) links in the field where densities are often much lower or habitat complexity is increased compared to laboratory settings [(Munyaneza & Obrycki 1997; Hohberg & Traunspurger 2005); see chapter 2.5.]. In nature, predators will encounter the small, abundant prey with much higher frequency than the rarer individuals of larger species. Therefore it seems reasonable for predators, to forage on small prey not all the time but when the net energy gain that the predator might get from the population of smaller prey is beyond a certain threshold level, i.e., at high enough densities of these small prey. It has been suggested that the biological mechanisms that are associated with sigmoid response curves relate to active changes between different foraging modes [e.g., the classical prey switching experiments where predatory fish were “forced” to forage either on the water surface or at the bottom of the aquarium dependent on the relative resources densities of flies (on surface) and worms (at the bottom) (Murdoch *et al.* 1975)]. Regarding the results from my experiments I propagate that also in simplified environments with only one prey species active changes in foraging behaviour at threshold levels seem plausible which has been suggested before (Hassell *et al.* 1977; Sih 1984). Moreover, this might be connected to traditional, functional classifications of consumers: for omnivorous consumers a size-related shift between different types of feeding seems biologically reasonable. Hence, a “predator” that usually attacks single individuals of prey organisms that are ten to hundred times smaller than itself (Brose *et al.* 2006a) could “switch” to being a “grazer” feeding on clouds or lawns of prey individuals ten-thousand times smaller (see box 1.2). This concept of consumers that are classified as belonging to a certain functional group but are able to switch to alter feeding mode drastically in situations of scarce preferred resources has been shown before for certain species of *Daphnia* (Horton *et al.* 1979). Relating these potential switching mechanisms to the body-size ratio and

the functional-response continua that I have specified before, I suggest the analogous term of the *grazer-predator continuum*, that is, in turn, closely connected to the consumer-resource size-ratios. To understand this concept mechanistically, one can imagine that consumer types from both ends of this continuum should be evolutionary optimised for their "standard" feeding strategy but in situations of resource scarcity they are able to apply other means of foraging. Interestingly, as detritivores have also been classified as grazers (Meehan 2006), this applies in a certain way to the predatory beetles in my experiments that are also known to be omnivorous (Harvey *et al.* 2008). Another mechanism that might be accountable for the preponderance of weak links (formed by sigmoid responses and reduced feeding rates as explained above) in the field is related to the phenology of predators and prey (Otto *et al.* 2008): Short-term peaks in interaction strengths might be relativised in the long run. This concept is supported by analyses of field-functional responses of predatory fishes where the passive switching is coupled to synchronous co-occurrence of predators and different prey species (Kempf *et al.* 2008). However, the relation between short-term and long-term interaction strengths is a field were additional research is urgently needed.

In conclusion and once more, I want to highlight the conceptual approach of this thesis, because there are numerous advantages where ecologists and biologists might benefit. On the one hand, if we envision the impossibility if we wanted to quantify exactly every single interaction in nature discouragement would be truly appropriate. On the other hand, there are countless phenomena in biology that are better described by continuous frameworks rather than fixed categories. Although thinking in categories has brought the biological sciences a far way from the early natural philosophers like Aristotle to the Human Genome Project, its limitations are obvious. First, the majority of categories we use to deal with in ecology and evolution turn out to be misleading or false in the majority of cases [e.g., the *species problem* (Hey 2001)]. Second, and even more problematic, many of our greatest problems regarding biodiversity conservation and future food security for mankind urgently need more knowledge about critical ecosystem processes. That is where the conceptual progress by applying body size as the first choice of a "classifying without classes" approach has outstanding advantages. I have shown in this thesis that conscious, careful yet targeted approaches of simplifying and conceptualising complexity are well-suited to explain natural phenomena. Finally, this might help to get critical insights how ecosystems are organised and how they are best-protected.

4. Bibliography

Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology & Evolution*, **15**, 337–341.

Albert, A.M. (1983) Characteristics of two populations of Lithobiidae (Chilopoda) determined in the laboratory and their relevance with regard to their ecological role as predators. *Zoologischer Anzeiger*, **211**, 214–226.

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P.G.P. & Hellgren, O. (2007) Flight speeds among bird species: Allometric and phylogenetic effects. *PLoS Biology*, **5**, e197.

Aljetlawi, A.A., Sparrevik, E. & Leonardsson, K. (2004) Prey-predator size-dependent functional response: derivation and rescaling to the real world. *Journal of Animal Ecology*, **73**, 239-252.

Andersen, K.H. & Beyer, J.E. (2006) Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist*, **168**, 54–61.

Arim, M., Abades, S.R., Laufer, G., Loureiro, M. & Marquet, P.A. (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos*, **119**, 147–153.

Bacher, S. (2012) Still not enough taxonomists: reply to Joppa et al. *Trends in Ecology & Evolution*, **27**, 65–66; author reply 66.

Bence, J.R. & Murdoch, W.W. (1986) Prey size selection by the mosquitofish: relation to optimal diet theory. *Ecology*, **67**, 324–336.

Bengtsson, J., Persson, T. & Lundkvist, H. (1997) Long-term effects of logging residue addition and removal on macroarthropods and Enchytraeids. *Journal of Applied Ecology*, **34**, 1014–1022.

Benton, T.G., Plaistow, S.J. & Coulson, T.N. (2006) Complex population dynamics and complex causation: Devils, details and demography. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1173–1181.

Berlow, E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature*, **398**, 330-334.

Berlow, E.L., Brose, U. & Martinez, N.D. (2008) The "Goldilocks factor" in food webs. *Proceedings of the National Academy of Sciences*, **105**, 4079-4080.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009) Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences*, **106**, 187 –191.

Berlow, E.L., Navarrete, S.A., Briggs, C., Power, M.E. & Menge, B. (1999) Quantifying variation in the strengths of species interactions. *Ecology*, **80**, 2206?2224.

Berlow, E.L., Neutel, A., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W., Jansen, V.A.A., Iwan Jones, J., Kokkoris, G.D., Logofet, D.O., McKane, A.J., Montoya, J.M. & Petchey, O. (2004) Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, **73**, 585-598.

Bernstein, C. (2000) Host-parasitoid models: the story of a successful failure. *Parasitoid Population Biology* (eds M.E. Hochberg & A.R. Ives), pp. 41–57. Princeton University Press, Princeton.

Berryman, A.A. (1992) The origins and evolution of predator-prey theory. *Ecology*, **73**, 1530–1535.

Bersier, L., Banasek-Richter, C. & Cattin, M. (2002) Quantitative descriptors of food-web matrices. *Ecology*, **83**, 2394-2407.

Bersier, L.-F. & Kehrli, P. (2008) The signature of phylogenetic constraints on food-web structure. *Ecological Complexity*, **5**, 132–139.

Binzer, A., Brose, U., Curtsdotter, A., Eklöf, A., Rall, B.C., Riede, J.O. & de Castro, F. (2011) The susceptibility of species to extinctions in model communities. *Basic and Applied Ecology*, **12**, 590–599.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J. & Benoît, E. (2009) How does abundance scale with body size in coupled size-structured food webs? *Journal of Animal Ecology*, **78**, 270–280.

Blanchard, J.L., Mills, C., Jennings, S., Fox, C.J., Rackham, B.D., Eastwood, P.D. & O'Brien, C.M. (2005) Distribution–abundance relationships for North Sea Atlantic cod (*Gadus morhua*): Observation versus theory. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2001–2009.

Boero, F. (2010) The study of species in the era of biodiversity: A tale of stupidity. *Diversity*, **2**, 115–126.

Bolker, B. (2008) *Ecological Models and Data in R*. Princeton University Press, Princeton.

Brooks, J.L. & Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science*, **150**, 28 –35.

Brose, U. (2008) Complex food webs prevent competitive exclusion among producer species. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2507 –2514.

Brose, U. (2010) Body-mass constraints on foraging behavior determine population and food-web dynamics. *Functional Ecology*, **24**, 28–34.

Brose, U., Berlow, E.L. & Martinez, N.D. (2005) Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters*, **8**, 1317-1325.

Brose, U., Ehnes, R., Rall, B., Vucic-Pestic, O., Berlow, E. & Scheu, S. (2008) Foraging theory predicts predator-prey energy fluxes. *Journal of Animal Ecology*, **77**, 1072-1078.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.C., Cushing, L., Dawah, H.A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G. & Cohen, J.E. (2006a) Consumer-resource body-size relationships in natural food webs. *Ecology*, **87**, 2411-2417.

Brose, U., Williams, R.J. & Martinez, N.D. (2006b) Allometric scaling enhances stability in complex food webs. *Ecology Letters*, **9**, 1228-1236.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.

Byström, P., Persson, L., Wahlström, E. & Westman, E. (2003) Size- and density-dependent habitat use in predators: consequences for habitat shifts in young fish. *Journal of Animal Ecology*, **72**, 156–168.

Carbone, C., Mace, G.M., Roberts, S.C. & Macdonald, D.W. (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature*, **402**, 286–288.

Carnicer, J., Abrams, P. & Jordano, P. (2008) Switching behavior, coexistence and diversification: comparing empirical community-wide evidence with theoretical predictions. *Ecology Letters*, **11**, 802–808.

Cattin, M.F., Bersier, L.F., Banasek-Richter, C., Baltensperger, R. & Gabriel, J.P. (2004) Phylogenetic constraints and adaptation explain food-web structure. *Nature*, **427**, 835-839.

Chen, B. & Wise, D.H. (1997) Responses of forest-floor fungivores to experimental food enhancement. *Pedobiologia*, **41**, 240–250.

Chen, B. & Wise, D.H. (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology*, **80**, 761–772.

Cohen, A.C. (1995) Extra-oral digestion in predaceous terrestrial Arthropoda. *Annual Review of Entomology*, **40**, 85–103.

Cohen, J., Jonsson, T. & Carpenter, S. (2003) Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 1781–1786.

Cohen, J.E., Pimm, S.L., Yodzis, P. & Saldana, J. (1993) Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, **62**, 67–78.

Colton, T. (1987) Extending functional-response models to include a 2nd prey type - an experimental test. *Ecology*, **68**, 900–912.

Colwell, R.K. & Lees, D.C. (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution*, **15**, 70–76.

Crawley, M.J. (1992) *Natural enemies: The population biology of predators, parasites, and diseases*. Blackwell Scientific Publications, Oxford.

Creer, S., Fonseca, V.G., Porazinska, D.L., Giblin-Davis, R.M., Sung, W., Power, D.M., Packer, M., Carvalho, G.R., Blaxter, M.L., Lambshead, P.J.D. & Thomas, W.K. (2010) Ultrasequencing of the meiofaunal biosphere: practice, pitfalls and promises. *Molecular Ecology*, **19**, 4–20.

Daan, N. (1973) A quantitative analysis of the food intake of North Sea cod, *Gadus Morhua*. *Netherlands Journal of Sea Research*, **6**, 479–517.

Damuth, J. (1981) Population density and body size in mammals. *Nature*, **290**, 699–700.

Dunger, W. (2008) *Tiere Im Boden*, 4th ed. Westarp Wissenschaften, Hohenwarsleben.

Ebenman, B. (1989) *Size-Structured Populations: Ecology and Evolution*, 1st ed (ed L Persson). Springer-Verlag.

Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Phylogenetic grouping, curvature and

metabolic scaling in terrestrial invertebrates. *Ecology Letters*, **14**, 993–1000.

Elliott, J. (2004) Prey switching in four species of carnivorous stoneflies. *Freshwater Biology*, **49**, 709-720.

Elliott, J. (2006) Prey switching in Rhyacophila dorsalis (Trichoptera) alters with larval instar. *Freshwater Biology*, **51**, 913–924.

Elliott, J.M. & Persson, L. (1978) The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology*, **47**, 977–991.

Elner, R.W. & Hughes, R.N. (1978) Energy maximization in diet of shore crab, Carcinus maenas. *Journal of Animal Ecology*, **47**, 103–116.

Elser, J.J., Fagan, W.F., Denno, R.F., Dobberfuhl, D.R., Folarin, A., Huberty, A., Interlandi, S., Kilham, S.S., McCauley, E., Schulz, K.L., Siemann, E.H. & Sterner, R.W. (2000) Nutritional constraints in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

Elton, C.S. (1927) *Animal Ecology*, 2001 Reprint. University of Chicago Press, Chicago.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.

Emlen, J.M. (1966) The role of time and energy in food preference. *The American Naturalist*, **100**, 611–617.

Emmerson, M.C. & Raffaelli, D. (2004) Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, **73**, 399-409.

Englund, G., Öhlund, G., Hein, C.L. & Diehl, S. (2011) Temperature dependence of the functional response. *Ecology Letters*, **14**, 914–921.

Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.-D. & Weisser, W.W. (2010) Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology*, **11**, 473–485.

Foelix, R.F. (1996) *Biology of Spiders*. Oxford University Press.

Fontaine, C., Guimarães Jr, P.R., Kéfi, S., Loeuille, N., Memmott, J., van der

Putten, W.H., van Veen, F.J.F. & Thébault, E. (2011) The ecological and evolutionary implications of merging different types of networks. *Ecology Letters*, **14**, 1170–1181.

Fryxell, J.M., Mosser, A., Sinclair, A.R.E. & Packer, C. (2007) Group formation stabilizes predator-prey dynamics. *Nature*, **449**, 1041–1043.

Fussmann, G.F. & Blasius, B. (2005) Community response to enrichment is highly sensitive to model structure. *Biology Letters*, **1**, 9–12.

Galarowicz, T.L. & Wahl, D.H. (2005) Foraging by a young-of-the-year piscivore: the role of predator size, prey type, and density. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2330–2342.

Galassi, M. (2009) *GNU Scientific Library: reference manual for GSL version 1.12*. Network Theory, Bristol.

Gardner, M.R. & Ashby, W.R. (1970) Connectance of Large Dynamic (Cybernetic) Systems: Critical Values for Stability. *Nature*, **228**, 784–784.

Gentleman, W., Leising, A., Frost, B., Strom, S. & Murray, J. (2003) Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **50**, 2847–2875.

Gentleman, W.C. & Neuheimer, A.B. (2008) Functional responses and ecosystem dynamics: How clearance rates explain the influence of satiation, food-limitation and acclimation. *Journal of Plankton Research*, **30**, 1215–1231.

Gergs, A. & Ratte, H.T. (2009) Predicting functional response and size selectivity of juvenile *Notonecta maculata* foraging on *Daphnia magna*. *Ecological Modelling*, **220**, 3331–3341.

Glazier, D.S. (2010) A unifying explanation for diverse metabolic scaling in animals and plants. *Biological Reviews*, **85**, 111–138.

Greenstone, M.H. (1979) Spider feeding behaviour optimises dietary essential amino acid composition. *Nature*, **282**, 501–503.

Gross, T., Rudolf, L., Levin, S.A. & Dieckmann, U. (2009) Generalized models reveal stabilizing factors in food webs. *Science*, **325**, 747 –750.

Häckel, E.H.P.A. (1866) *Generelle Morphologie Der Organismen. Allgemeine Grundzüge Der Organischen Formen-Wissenschaft, Mechanisch Begründet Durch Die Von Charles Darwin Reformierte Descendenztheorie*. G. Reimer, Berlin.

Halaj, J., Peck, R.W. & Niwa, C.G. (2005) Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: a stable isotope analysis with $\delta^{15}N$ and $\delta^{13}C$. *Pedobiologia*, **49**, 109–118.

Hansen, P.J., Bjornsen, P.K. & Hansen, B.W. (1997) Zooplankton grazing and growth: Scaling within the 2-2,000-µm body size range. *Limnology and Oceanography*, **42**, 687–704.

Harvey, J.A., van der Putten, W.H., Turin, H., Wagenaar, R. & Bezemer, T.M. (2008) Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds. *Agriculture, Ecosystems & Environment*, **127**, 100–106.

Hassell, M.P. (1978) *The Dynamics of Arthropod Predator-prey Systems*. Princeton University Press, Princeton.

Hassel, M., Lawton, J. & Beddington, J. (1976) Components of arthropod predation: I. The prey death-rate. *Journal of Animal Ecology*, **45**, 135-164.

Hassell, M.P., Lawton, J.H. & Beddington, J.R. (1977) Sigmoid functional responses by invertebrate predators and parasitoids. *Journal of Animal Ecology*, **46**, 249–262.

Hauzy, C., Tully, T., Spataro, T., Paul, G. & Arditi, R. (2010) Spatial heterogeneity and functional response: an experiment in microcosms with varying obstacle densities. *Oecologia*, **163**, 625–636.

Hendriks, A.J. (1999) Allometric scaling of rate, age and density parameters in ecological models. *Oikos*, **86**, 293–310.

Hewett, S.W. (1980) The effect of prey size on the functional and numerical responses of a protozoan predator to its prey. *Ecology*, **61**, 1075–1081.

Hey, J. (2001) The mind of the species problem. *Trends in Ecology & Evolution*, **16**, 326–329.

Hirvonen, H. & Ranta, E. (1996) Prey to predator size ratio influences foraging efficiency of larval *Aeshna juncea* dragonflies. *Oecologia*, **106**, 407–415.

Hjelm, J. & Persson, L. (2001) Size-dependent attack rate and handling capacity: inter-cohort competition in a zooplanktivorous fish. *Oikos*, **95**, 520–532.

Hoddle, M. (2003) The effect of prey species and environmental complexity on the functional response of *Franklinothrips orizabensis*: a test of the fractal foraging model. *Ecological Entomology*, **28**, 309–318.

Hohberg, K. & Traunspurger, W. (2005) Predator–prey interaction in soil food web: functional response, size-dependent foraging efficiency, and the influence of soil texture. *Biology and Fertility of Soils*, **41**, 419–427.

Holling, C. (1959) Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist*, **91**, 385-398.

Holling, C.S. (1959b) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, **91**, 293–320.

Horton, P.A., Rowan, M., Webster, K.E. & Peters, R.H. (1979) Browsing and grazing by cladoceran filter feeders. *Canadian Journal of Zoology*, **57**, 206–212.

Houde, E.D. & Schekter, R.C. (1980) Feeding by marine fish larvae: developmental and functional responses. *Environmental Biology of Fishes*, **5**, 315–334.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Hughes, R. & Croy, M. (1993) An experimental analysis of frequency-dependent predation (switching) in the 15-spined stickleback, *Spinachia spinachia*. *Journal of Animal Ecology*, **62**, 341–352.

Ings, T.C., Montoya, J.M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C.F., Edwards, F., Figueroa, D., Jacob, U., Jones, J.I., Lauridsen, R.B., Ledger, M.E., Lewis, H.M., Olesen, J.M., van Veen, F.J.F., Warren, P.H. & Woodward, G. (2009) Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, **78**, 253–269.

Isaac, N.J.B. & Carbone, C. (2010) Why are metabolic scaling exponents so controversial? Quantifying variance and testing hypotheses. *Ecology Letters*, **13**, 728–735.

Ives, A.R. & Godfray, H.C.J. (2006) Phylogenetic analysis of trophic associations. *The American Naturalist*, **168**, E1–E14.

Jennings, S. & Blanchard, J.L. (2004) Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*, **73**, 632–642.

Jennings, S. & Mackinson, S. (2003) Abundance–body mass relationships in size-structured food webs. *Ecology Letters*, **6**, 971–974.

Jensen, K., Mayntz, D., Toft, S., Clissold, F.J., Hunt, J., Raubenheimer, D. & Simpson, S.J. (2012) Optimal foraging for specific nutrients in predatory beetles. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 2212-2218.

Jeschke, J.M., Kopp, M. & Tollrian, R. (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, **72**, 95–112.

Jeschke, J., Kopp, M. & Tollrian, R. (2004) Consumer-food systems: why type I functional responses are exclusive to filter feeders. *Biological Reviews*, **79**, 337–349.

Jeschke, J.M. & Tollrian, R. (2005a) Predicting Herbivore Feeding Times. *Ethology*, **111**, 187–206.

Jeschke, J.M. & Tollrian, R. (2005b) Effects of predator confusion on functional responses. *Oikos*, **111**, 547–555.

Juliano, S.A. (2001) Non-linear curve fitting: predation and functional response curves. *Design and Analysis of Ecological Experiments*, 2nd ed (eds S.M. Scheiner & J. Gurevitch), pp. 178–216. Oxford University Press.

Kaiser, H. (1983) Small scale spatial heterogeneity influences predation success in an unexpected way: Model experiments on the functional response of predatory mites (Acarina). *Oecologia*, **56**, 249–256.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C. & Brose, U. (2012) More than a meal… integrating non-feeding interactions into food webs. *Ecology Letters*, **15**, 291–300.

Kempf, A., Floeter, J. & Temming, A. (2008) Predator–prey overlap induced Holling type III functional response in the North Sea fish assemblage. *Marine Ecology Progress Series*, **367**, 295–308.

Kempson, D., Lloyd, M. & Ghelardi, R. (1963) A new extractor for woodland litter. *Pedobiologia*, **3**, 1–21.

Kerr, S.R. (1974) Theory of size distribution in ecological communities. *Journal of the Fisheries Research Board of Canada*, **31**, 1859–1862.

King, R.A., Read, D.S., Traugott, M. & Symondson, W.O.C. (2008) Molecular analysis of predation: a review of best practice for DNA-based approaches. *Molecular Ecology*, **17**, 947–963.

Kleiber, M. (1932) Body size and metabolism. *Hilgardia*, **6**, 315–353.

Koch, R.L., Hutchison, W.D., Venette, R.C. & Heimpel, G.E. (2003) Susceptibility of immature monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae: Danainae), to predation by *Harmonia axyridis* (Coleoptera: Coccinellidae). *Biological Control*, **28**, 265–270.

Koen-Alonso, M. (2007) A Process-Oriented Approach to the Multispecies Functional Response. *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems*. The Peter Yodzis fundamental Ecology Series. pp. 1-36. Springer.

Kolokotrones, T., Savage, V., Deeds, E.J. & Fontana, W. (2010) Curvature in metabolic scaling. *Nature*, **464**, 753–756.

Kondoh, M. (2003) Foraging adaptation and the relationship between food-web complexity and stability. *Science*, **299**, 1388 –1391.

Kratina, P., Vos, M. & Anholt, B.R. (2007) Species diversity modulates predation. *Ecology*, **88**, 1917–1923.

Kratina, P., Vos, M., Bateman, A. & Anholt, B.R. (2009) Functional responses modified by predator density. *Oecologia*, **159**, 425–433.

Krebs, C.J. (2001) *Ecology*, Fifth ed. Benjamin Cummings, San Francisco.

Landry, M. (1981) Switching between herbivory and carnivory by the planktonic marine copepod Calanus pacificus. *Marine Biology*, **65**, 77–82.

Lang, B., Rall, B.C. & Brose, U. (2012) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, **81**, 516–523.

Law, R., Plank, M.J., James, A. & Blanchard, J.L. (2009) Size-spectra dynamics from stochastic predation and growth of individuals. *Ecology*, **90**, 802–811.

Lawrence, K.L. & Wise, D.H. (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia*, **44**, 33–39.

Leslie, P.H. (1958) A stochastic model for studying the properties of certain biological systems by numerical methods. *Biometrika*, **45**, 16–31.

Loeuille, N. & Loreau, M. (2005) Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 5761–5766.

Lotka, A.J. (1925) *Elements of Physical Biology*. Williams and Watkins, Baltimore, MD.

MacArthur, R. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology*, **36**, 533-536.

MacArthur, R.H. & Pianka, E.R. (1966) On optimal use of a patchy environment. *The American Naturalist*, **100**, 603–609.

Macfadyen, A. (1961) Improved funnel-type extractors for soil arthropods. *Journal of Animal Ecology*, **30**, 171–184.

Malthus, T. (1798) *An Essay on the Principle of Population*, 1999 reprint. Oxford University Press, Oxford.

Marquet, P.A., Quiñones, R.A., Abades, S., Labra, F., Tognelli, M., Arim, M. & Rivadeneira, M. (2005) Scaling and power-laws in ecological systems. *Journal of Experimental Biology*, **208**, 1749–1769.

May, R.M. (1972) Will a large complex system be stable. *Nature*, **238**, 413-414.

May, R.M. (1974) Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. *Science*, **186**, 645–647.

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. & Simpson, S.J. (2005) Nutrient-specific foraging in invertebrate predators. *Science*, **307**, 111–113.

McCann, K. (2000) The diversity-stability debate. *Nature*, **405**, 228-233.

McCann, K.S., Hastings, A. & Huxel, G.R. (1998) Weak trophic interactions and the balance of nature. *Nature*, **395**, 794-798.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005) The dynamics of spatially coupled food webs. *Ecology Letters*, **8**, 513–523.

McCann, K. & Yodzis, P. (1994) Biological conditions for chaos in a three-species food chain. *Ecology*, **75**, 561-564.

Mckee, M., Wrona, F., Scrimgeour, G. & Culp, J. (1997) Importance of consumptive and non-consumptive prey mortality in a coupled predator-prey system. *Freshwater Biology*, **38**, 193–201.

McLaughlin, O.B., Jonsson, T. & Emmerson, M.C. (2010) Temporal variability in predator-prey relationships of a forest floor food web. *Advances in Ecological Research: Ecological Networks* (ed G. Woodward), pp. 171–264.

Elsevier Academic Press Inc, San Diego.

Meehan, T.D. (2006) Energy use and animal abundance in litter and soil communities. *Ecology*, **87**, 1650-1658.

Messier, F. (1994) Ungulate population models with predation: a case study with the North American moose. *Ecology*, **75**, 478–488.

Mittelbach, G.G. (1981) Foraging efficiency and body size: A study of optimal diet and habitat use by bluegills. *Ecology*, **62**, 1370–1386.

Montoya, J.M., Pimm, S.L. & Sole, R.V. (2006) Ecological networks and their fragility. *Nature*, **442**, 264, 259.

Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011) How many species are there on earth and in the ocean? *PLoS Biology*, **9**, e1001127.

Moulder, B.C. & Reichle, D.E. (1972) Significance of spider predation in the energy dynamics of forest-floor arthropod communities. *Ecological Monographs*, **42**, 473–498.

Mulder, C., Den Hollander, H., Vonk, J., Rossberg, A., Jagers op Akkerhuis, G. & Yeates, G. (2009) Soil resource supply influences faunal size–specific distributions in natural food webs. *Naturwissenschaften*, **96**, 813–826.

Munyaneza, J. & Obrycki, J.J. (1997) Functional response of *Coleomegilla maculata* (Coleoptera: Coccinellidae) to Colorado potato beetle eggs (Coleoptera: Chrysomelidae). *Biological Control*, **8**, 215–224.

Murdoch, W.W. (1969) Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecological Monographs*, **39**, 335–354.

Murdoch, W.W. (1973) Functional response of predators. *Journal of Applied Ecology*, **10**, 335–342.

Murdoch, W.W., Avery, S. & Smyth, M.E.B. (1975) Switching in predatory fish. *Ecology*, **56**, 1094–1105.

Murdoch, W.W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research*, **9**, 1-131.

Nee, S., Read, A.F., Greenwood, J.J.D. & Harvey, P.H. (1991) The relationship between abundance and body size in British birds. *Nature*, **351**, 312–313.

Neutel, A., Heesterbeek, J.A.P., van de Koppel, J., Hoenderboom, G., Vos, A.,

Kaldeway, C., Berendse, F. & de Ruiter, P.C. (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature*, **449**, 599-602.

Neutel, A., Heesterbeek, J.A.P. & de Ruiter, P.C. (2002) Stability in real food webs: Weak links in long loops. *Science*, **296**, 1120-1123.

Newman, J.A., Parsons, A.J., Thornley, J.H.M., Penning, P.D. & Krebs, J.R. (1995) Optimal diet selection by a generalist grazing herbivore. *Functional ecology*, **9**, 255–268.

Oaten, A. & Murdoch, W.W. (1975a) Switching, functional response, and stability in predator-prey systems. *The American Naturalist*, **109**, 299–318.

Oaten, A. & Murdoch, W.W. (1975b) Functional response and stability in predator-prey systems. *The American Naturalist*, **109**, 289–298.

Oelbermann, K. & Scheu, S. (2010) Trophic guilds of generalist feeders in soil animal communities as indicated by stable isotope analysis ($^{15}N/^{14}N$). *Bulletin of Entomological Research*, **100**, 511–520.

Otto, S., Berlow, E., Rank, N., Smiley, J. & Brose, U. (2008) Predator diversity and identity drive interaction strength and trophic cascades in a food web. *Ecology*, **89**, 134–144.

Otto, S., Rall, B.C. & Brose, U. (2007) Allometric degree distributions stabilize food webs. *Nature*, **450**, 1226-1229.

Paine, R.T. (1980) Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology*, **49**, 667–685.

Persson, L., Leonardsson, K., de Roos, A., Gyllenberg, M. & Christensen, B. (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model. *Theoretical Population Biology*, **54**, 270-293.

Persson, L., Roos, D., M, A., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, E. & Westman, E. (2003) Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences*, **100**, 4035–4039.

Pervez, A. & Omkar. (2005) Functional responses of coccinellid predators: An illustration of a logistic approach. *Journal of Insect Science*, **5**, 6pp.

Peschel, K., Norton, R.A., Scheu, S. & Maraun, M. (2006) Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite *Pergamasus septentrionalis*. *Soil Biology and Biochemistry*,

38, 2985–2989.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008) Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*, **105**, 4191-4196.

Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2011) Fit, efficiency, and biology: Some thoughts on judging food web models. *Journal of Theoretical Biology*, **279**, 169–171.

Petchey, O.L. & Belgrano, A. (2010) Body-size distributions and size-spectra: Universal indicators of ecological status? *Biology Letters*, **6**, 434–437.

Peters, R.H. (1983) *The ecological implications of body size*. Cambridge University Press.

Pimm, S.L. (1984) The complexity and stability of ecosystems. *Nature*, **307**, 321–326.

Pimm, S., Lawton, J. & Cohen, J. (1991) Food web patterns and their consequences. *Nature*, **350**, 669–674.

Pisani, D., Poling, L., Lyons-Weiler, M. & Hedges, S. (2004) The colonization of land by animals: Molecular phylogeny and divergence times among arthropods. *BMC Biology*, **2**, 1.

Pitt, W.C. & Ritchie, M.E. (2002) Influence of prey distribution on the functional response of lizards. *Oikos*, **96**, 157–163.

Polis, G. (1991) Complex trophic interactions in deserts - an empirical critique of food-web theory. *The American Naturalist*, **138**, 123–155.

Polis, G. & Strong, D. (1996) Food web complexity and community dynamics. *The American Naturalist*, **147**, 813–846.

Ponsard, S., Arditi, R. & Jost, C. (2000) Assessing top-down and bottom-up control in a litter-based soil macroinvertebrate food chain. *Oikos*, **89**, 524–540.

Post, D.M. (2002) Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology*, **83**, 703–718.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996) Challenges in the quest for keystones. *Bioscience*, **46**, 609–620.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977) Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, **52**, 137–154.

R Development Core Team. (2009) *R: A Language and Environment for Statistical Computing*. Vienna, Austria.

Raffaelli, D. (2007) Food webs, body size and the curse of the latin binomial. *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems (Eds.: Neil Rooney, K. S. McCann and D. L. G. Noakes)* The Peter Yodzis fundamental ecology series. pp. 53–64. Springer, Dordrecht.

Raffaelli, D., Solan, M. & Webb, T.J. (2005) Do marine and terrestrial ecologists do it differently? Bridging the gap between aquatic and terrestrial ecology. *Marine ecology progress series*, **304**, 283–289.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O. & Petchey, O.L. (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2923–2934.

Rall, B.C., Guill, C. & Brose, U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, **117**, 202-213.

Rall, B.C., Kalinkat, G., Ott, D., Vucic-Pestic, O. & Brose, U. (2011) Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos*, **120**, 483–492.

Rall, B.C., Vucic-Pestic, O., Ehnes, R.B., Emmerson, M.C. & Brose, U. (2010) Temperature, predator-prey interaction strength and population stability. *Global Change Biology*, **16**, 2145–2157.

Real, L. (1977) Kinetics of functional response. *American Naturalist*, **111**, 289-300.

Real, L.A. (1979) Ecological determinants of functional response. *Ecology*, **60**, 481–485.

Reuman, D.C., Mulder, C., Raffaelli, D. & Cohen, J.E. (2008) Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecology Letters*, **11**, 1216–1228.

Rezende, E.L., Lavabre, J.E., Guimaraes, P.R., Jordano, P. & Bascompte, J. (2007) Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, **448**, 925–928.

Rickers, S. & Scheu, S. (2005) Cannibalism in *Pardosa palustris* (Araneae,

Lycosidae): effects of alternative prey, habitat structure, and density. *Basic and Applied Ecology*, **6**, 471–478.

Riede, J.O., Brose, U., Ebenman, B., Jacob, U., Thompson, R., Townsend, C.R. & Jonsson, T. (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecology Letters*, **14**, 169–178.

Ritz, C. & Streibig, J.C. (2009) *Nonlinear Regression with R*, 1st ed. Springer US, New York.

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369-&.

Rooney, N., McCann, K., Gellner, G. & Moore, J.C. (2006) Structural asymmetry and the stability of diverse food webs. *Nature*, **442**, 265–269.

De Roos, A. & Persson, L. (2002) Size-dependent life-history traits promote catastrophic collapses of top predators. *Proceedings of the National Academy of Sciences*, **99**, 12907–12912.

Roughgarden, J. (1983) Competition and theory in community ecology. *The American Naturalist*, **122**, 583–601.

Royama, T. (1971) A comparative study of models for predation and parasitism. *Researches on Population Ecology*, **13**, 1–91.

Rudolf, V.H.W. (2006) The influence of size-specific indirect interactions in predator–prey systems. *Ecology*, **87**, 362–371.

Rudolf, V.H.W. (2008a) Impact of cannibalism on predator–prey dynamics: size-structured interactions and apparent mutualism. *Ecology*, **89**, 1650–1660.

Rudolf, V.H.W. (2008b) Consequences of size structure in the prey for predator-prey dynamics: the composite functional response. *Journal of Animal Ecology*, **77**, 520–528.

Rudolf, V. & Armstrong, J. (2008) Emergent impacts of cannibalism and size refuges in prey on intraguild predation systems. *Oecologia*, **157**, 675–686.

Ruess, L. & Chamberlain, P.M. (2010) The fat that matters: Soil food web analysis using fatty acids and their carbon stable isotope signature. *Soil Biology and Biochemistry*, **42**, 1898–1910.

de Ruiter, P., Neutel, A. & Moore, J. (1995) Energetics, patterns of interaction

strengths, and stability in real ecosystems. *Science*, **269**, 1257-1260.

Samish, M. & Rehacek, J. (1999) Pathogens and predators of ticks and their potential in biological control. *Annual review of entomology*, **44**, 159–182.

Sarnelle, O. & Wilson, A.E. (2008) Type III functional response in *Daphnia*. *Ecology*, **89**, 1723–1732.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004) Effects of body size and temperature on population growth. *The American Naturalist*, **163**, 429–441.

Schaefer, M. (1990) The soil fauna of a beech forest on limestone: trophic structure and energy budget. *Oecologia*, **82**, 128–136.

Scheffer, M. & De Boer, R.J. (1995) Implications of spatial heterogeneity for the paradox of enrichment. *Ecology*, **76**, 2270–2277.

Schenk, D. & Bacher, S. (2002) Functional response of a generalist insect predator to one of its prey species in the field. *Journal of Animal Ecology*, **71**, 524–531.

Schenk, D., Bersier, L.-F. & Bacher, S. (2005) An experimental test of the nature of predation: neither prey- nor ratio-dependent. *Journal of Animal Ecology*, **74**, 86–91.

Scheu, S. (2001) Plants and generalist predators as links between the below-ground and above-ground system. *Basic and Applied Ecology*, **2**, 3–13.

Scheu, S. (2002) The soil food web: structure and perspectives. *European Journal of Soil Biology*, **38**, 11–20.

Scheu, S. & Falca, M. (2000) The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofauna-dominated community. *Oecologia*, **123**, 285–296.

Scheu, S. & Schaefer, M. (1998) Bottom-up control of the soil macrofauna community in a beechwood on limestone: Manipulation of food resources. *Ecology*, **79**, 1573–1585.

Schmidt, M.H., Lauer, A., Purtauf, T., Thies, C., Schaefer, M. & Tscharntke, T. (2003) Relative importance of predators and parasitoids for cereal aphid control. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 1905–1909.

Sheldon, R.W., Sutcliff, Jr., W.H. & Prakash, A. (1972) The size distribution of

particles in the ocean. *Limnology and Oceanography*, **17**, 327–340.

Sih, A. (1984) Optimal behavior and density-dependent predation. *The American Naturalist*, **123**, 314–326.

Skalski, G.T. & Gilliam, J.F. (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, **82**, 3083–3092.

Smout, S. & Lindstrøm, U. (2007) Multispecies functional response of the minke whale *Balaenoptera acutorostrata* based on small-scale foraging studies. *Marine Ecology Progress Series*, **341**, 277–291.

Snell, O. (1892) Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen Fähigkeiten. *European Archives of Psychiatry and Clinical Neuroscience*, **23**, 436–446.

Soetaert, K., Petzoldt, T. & Setzer, R.W. (2010) Solving Differential Equations in R: Package deSolve. *Journal of Statistical Software*, **33**, 1–25.

Solomon, M.E. (1949) The natural control of animal populations. *Journal of Animal Ecology*, **18**, 1–35.

Spitze, K. (1985) Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. *Ecology*, **66**, 938-949.

Stephens, D.W. & Krebs, J.R. (1986) *Foraging Theory*. Princeton University Press, Princeton.

Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton.

Sundell, J., Eccard, J.A., Tiilikainen, R. & Ylönen, H. (2003) Predation rate, prey preference and predator switching: experiments on voles and weasels. *Oikos*, **101**, 615–623.

Symondson, W.O.C., Sunderland, K.D. & Greenstone, M.H. (2002) Can generalist predators be effective biocontrol agents? *Annual Review of Entomology*, **47**, 561–594.

Thompson, D.J. (1975) Towards a predator-prey model incorporating age structure - effects of *Daphnia magna* by *Ischnura elegans*. *Journal of Animal Ecology*, **44**, 907-916.

Troost, T., Kooi, B. & Dieckmann, U. (2008) Joint evolution of predator body size

and prey-size preference. *Evolutionary Ecology*, **22**, 771–799.

Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. & Dunne, J.A. (2010) Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecology Letters*, **13**, 1546–1559.

Vander Zanden, M.J. & Rasmussen, J.B. (2001) Variation in d15N and d13C trophic fractionation: Implications for aquatic food web studies. *Limnology and Oceanography*, **46**, 2061–2066.

Verhulst, P.-F. (1838) Notice sur la loi que la population suit dans son accroissement. *Correspondance Mathematique et Physique (Edited by A. Quetelet)*, **10**, 113–121.

Volterra, V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature*, 558–560.

Vonesh, J. & Bolker, B. (2005) Compensatory larval responses shift trade-offs associated with predator-induced hatching plasticity. *Ecology*, **86**, 1580–1591.

Vucic-Pestic, O., Birkhofer, K., Rall, B.C., Scheu, S. & Brose, U. (2010a) Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction. *Pedobiologia*, **53**, 307–312.

Vucic-Pestic, O., Ehnes, R.B., Rall, B.C. & Brose, U. (2011) Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Global Change Biology*, **17**, 1301–1310.

Vucic-Pestic, O., Rall, B.C., Kalinkat, G. & Brose, U. (2010b) Allometric functional response model: body masses constrain interaction strengths. *Journal of Animal Ecology*, **79**, 249–256.

Wahlström, E., Persson, L., Diehl, S. & Bystrom, P. (2000) Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia*, **123**, 138-148.

Weitz, J.S. & Levin, S.A. (2006) Size and scaling of predator–prey dynamics. *Ecology Letters*, **9**, 548–557.

Werner, E.E. & Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size−structured populations. *Annual review of ecology and systematics*, **15**, 393–425.

Werner, E.E. & Hall, D.J. (1974) Optimal Foraging and the Size Selection of Prey by the Bluegill Sunfish (*Lepomis Macrochirus*). *Ecology*, **55**, 1042.

West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122-126.

Western, D. (1979) Size, life history and ecology in mammals. *African Journal of Ecology*, **17**, 185–204.

Westoby, M. (1974) An analysis of diet selection by large generalist herbivores. *The American Naturalist*, **108**, 290–304.

Williams, R.J. & Martinez, N.D. (2000) Simple rules yield complex food webs. *Nature*, **404**, 180-183.

Williams, R.J. & Martinez, N.D. (2004a) Limits to trophic levels and omnivory in complex food webs: Theory and data. *The American naturalist*, **163**, 458–468.

Williams, R.J. & Martinez, N.D. (2004b) Stabilization of chaotic and non-permanent food-web dynamics. *European Physical Journal B*, **38**, 297-303.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J.M., Olesen, J.M., Valido, A. & Warren, P.H. (2005) Body size in ecological networks. *Trends in Ecology & Evolution*, **20**, 402–409.

Woodward, G. & Hildrew, A.G. (2002a) Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology*, **71**, 1063–1074.

Woodward, G. & Hildrew, A. (2002b) Differential vulnerability of prey to an invading top predator: integrating field surveys and laboratory experiments. *Ecological Entomology*, **27**, 732–744.

Wootton, J. & Emmerson, M. (2005) Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 419--444.

Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *The American Naturalist*, **139**, 1151–1175.

5. Summary

Many, if not all, ecosystems on earth are threatened by increasing human populations and resource-intensive economical growth entailing pollution, eutrophication and habitat fragmentation, to name some of the threats. As many of these ecosystems provide vital services for mankind there is an urgent need to understand how the populations and communities within these systems function, how their stability comes about and might be protected. Therefore we need more than knowledge about *diversity* (e.g., how many species are there) but, most critically, how the *complexity* of all interacting ecological entities (e.g., populations) is structured and constrained. To evaluate critical processes, the categorical, Linnean classification of biodiversity might hamper an ecosystem-wide approach resulting in generalised suggestions. Rather, we should address the interdependent dimensions of organisms' body-sizes and biomass flows as continuous variables being key to a better understanding of nature. Hence, this thesis was motivated by the findings of several recent and prominent studies that highlighted two aspects of community ecology: (1) There are general patterns in the body-size distributions within food webs that seem to prevail in ecosystems as different as a coral reef and a forest-floor. (2) These body-size relations in food webs have profound effects on the quality and quantity of the interactions that govern the flow of energy and nutrients within these webs and therefore are fundamental for our understanding of their dynamics and their stability.

To investigate generalities in body-size effects on interaction strengths I performed various laboratory experiments where prey-density dependent feeding rates of terrestrial arthropod predators were examined under different experimental settings. Accordingly, a model framework was established on the base of taxonomic predator-prey pairs with distinct size-ratios that unravelled particular size dependencies on the fundamental parameters (i.e., biological mechanisms) of the interactions (Chapter 2.1.). Furthermore, the statistical modelling approach was tailored to incorporate these findings in a framework where exclusion of taxonomic information is the next possible step providing the opportunity to build a global null model for the interactions of many species-pairs: In Chapter 2.2. I have shown how allometric information alone explains a large fraction of the variation in feeding rates although more complex models comprising taxonomic *and* allometric information perform better. Nevertheless, for the analyses of a much more comprehensive dataset in Chapter 2.3. I decided to skip taxonomic information for the sake of clarity and showed far-reaching

consequences on the community-level through the general existence of sigmoid response curves. One of the outstanding findings of this thesis is that these rules also comply with body-size relations of predator-prey pairs in natural food webs.

The experiments with systematic variance in predator and prey body sizes providing the database for the chapters 2.1. - 2.3. were build upon the simplifying assumption of an idealised environment with one predator and only one prey species per replicate and a constant level of habitat structure. In contrast, I increased the complexity of the experimental setting in the concluding two chapters: In Chapter 2.4. I tested how predictions from single-prey experiments presented in Chapter 2.1. are suitable to interpret the outcomes of more complex experiments with two different(-sized) prey species. I found that in contrast to the allometric null models larger predators favour larger prey to an unanticipated extent therefore potentially contributing to the mix of weak and strong interactions stabilising empirical food webs. Finally I tested how the effects of changing habitat structure (i.e., leaf litter) affects predator-prey interactions particularly in dynamically changing habitats (chapter 2.5.). It could be shown that alternating amounts of litter were translated into a dilution effect impairing predator-prey encounter rates and thereby reducing the potential for top-down control in litter-dominated systems to a minimum.

Altogether, the results in this thesis emphasise that the regular patterns of body-size distributions in nature are interdependent with the allometric constraints on the interactions that connect individuals and populations in food webs. Furthermore, active preferences towards larger, but usually rarer, prey together with habitat-structure effects might create the general framework where patterns of strong and weak feeding links promote the stability of natural communities. The diversity and intricacy of nature with millions of species connected by a multiple of interactions often leaves us ecologists with more questions than answers. Nevertheless, the approaches and results in this thesis suggest that complexity-reducing, quantitative model frameworks represent a suitable tool to understand how interactions are shaped and, accordingly, the functioning and stability of real ecosystems.

6. Zusammenfassung

Fast alle Ökosysteme weltweit sind heute durch menschliche Aktivitäten gefährdet. Da sie gleichzeitig lebenswichtige Funktionen für die globale Ernährung und das Wohlergehen der Menschheit sicherstellen, müssen wir dringend die entscheidenden Prozesse in Ökosystemen und ökologischen Gemeinschaften besser verstehen. Dabei ist es seit langem ein zentrales Anliegen zu verstehen, wie die Stabilität von Gemeinschaften und der von ihnen erbrachten Funktionen gewährleistet wird. Die vorliegende Arbeit knüpft dabei an viel beachtete, aktuelle Forschungsergebnisse an: (1.) Es gibt allgemeingültige Muster in den Körpergrößenverteilungen in Nahrungsnetzen. Diese scheinen so universell zu sein, dass sie in sehr unterschiedlichen Ökosystemen nachgewiesen werden konnten. (2.) Körpergrößenverhältnisse haben tiefgreifende Auswirkungen auf die Interaktionen zwischen Individuen, Populationen und Arten. Diese Interaktionen wiederum bestimmen, wie Energie und Nährstoffe durch Nahrungsnetze zirkulieren und sind deshalb von elementarer Bedeutung für Funktion und Stabilität von Ökosystemen.

Um generelle Muster von Körpergrößeneffekten bei Räuber-Beute-Interaktionen zu untersuchen, führte ich verschiedene Laborexperimente durch. Dabei habe ich die Beutedichte-abhängigen Fraßraten terrestrischer Gliederfüßer innerhalb verschiedener experimenteller Ansätze untersucht. Für die Analysen habe ich ein Interaktionsmodell konzipiert, mit dem ich anhand taxonomischer Räuber-Beute-Paare mit unterschiedlichen Körpergrößen-verhältnissen aufzeigen konnte, wie die maßgeblichen Parameter des Modells von den Körpergrößen abhängig sind (Kapitel 2.1.). In Kapitel 2.2. zeige ich dann, wie alleine anhand Körpergrößen-basierter Information ein großer Teil der Varianz in den Fraßraten erklärt werden konnte, auch wenn der komplexere Modellansatz der taxonomische *und* Größen-basierte Information miteinbezieht, bessere Ergebnisse lieferte. In einem weiteren Schritt in Kapitel 2.3. habe ich mit dem Ansatz aus Kapitel 2.2. einen wesentlich umfangreicheren Datensatz analysiert. Hier wurde der Einfachheit halber die taxonomische Information komplett außen vor gelassen. So konnte ich zeigen, dass die Körpergrößenverteilung in Nahrungsnetzen mit bestimmten, populationsdynamisch stabilisierenden Motiven in den Fraßraten einhergeht - den so genannten „Typ III functional responses“ oder „sigmoid responses“. Genau genommen werden diese stabilisierenden „sigmoid responses“ für große Räuber auf kleinen Beuten gefunden. Im Folgenden habe ich ein dementsprechend

erweitertes Interaktionsmodell in einer Modellsimulation von Populationsdynamiken angewandt. Ein herausragendes Ergebnis dieser Arbeit ist der anschließende Befund, dass die Ergebnisse der Simulation zu einem hohen Maße mit natürlichen Größenverhältnissen von Räuber-Beute-Paaren übereinstimmen. Die Experimente mit systematischer Varianz der Räuber- und Beutegrößen, welche die Datengrundlage für die Kapitel 2.1.- 2.3. geliefert haben, wurden allerdings in einfachen, reduktionistischen Versuchsanordnungen gewonnen. Um den Bedingungen in natürlichen Lebensräumen etwas näher zu kommen, habe ich in den beiden abschließenden Kapiteln den experimentellen Ansatz erweitert: In Kapitel 2.4. habe ich getestet, inwiefern Vorhersagen, die aus den einfacheren Modellen aus Kapitel 2.1. hergeleitet wurden, belastbar sind, wenn der Räuber zwischen zwei verschieden großen Beuten (in unterschiedlichen relativen Dichten) wählen kann. Anhand der Ergebnisse sowie konzeptioneller Ausführungen konnte ich zeigen, dass die Präferenzen für große Beuten über das vorhergesagte Maß hinausgingen (ich nenne dieses Phänomen hier „aktive Präferenz“). Zusammen mit den natürlichen Abundanzen großer und kleiner Beuten ergeben sich potentielle Muster von Fraßraten, die insgesamt zur Stabilität von Nahrungsnetzen beitragen können. In Kapitel 2.5. habe ich abschließend getestet, wie sich der Effekt von variierender Habitatstruktur auf eine typische Räuber-Beute-Interaktion des Bodennahrungsnetzes auswirkt. Ich konnte zeigen, dass variierende Mengen von Laubstreu sich in Form eines Verdünnungseffektes auf Räuber- und Beutedichten auswirken, was vor allem die Häufigkeit des Zusammentreffens von Räuber- und Beuteindividuen beeinflusst. Dieses Phänomen sorgt dafür, dass man in Ökosystemen mit großen Mengen Laubstreu nicht davon ausgehen kann, dass Beutepopulationen von Räubern kontrolliert werden.

In dieser Arbeit konnte ich zeigen, dass biologische, Körpergrößen-abhängige Mechanismen bei Räuber-Beute Beziehungen die Stabilität von Nahrungsnetzen bedingen. Darüber hinaus scheinen aktive Präferenzen für große Beuten zusammen mit Habitatstruktur-Effekten das typische Muster von wenigen starken und vielen schwachen Interaktionen in natürlichen, ökologischen Gemeinschaften zu erzeugen. Die Vielfalt und Komplexität der Natur mit Millionen von Arten und einem Vielfachen an Interaktionen zwischen diesen Arten hinterlässt uns Ökologen oftmals mit mehr Fragen als Antworten. Quantitative Modellansätze, welche die natürliche Komplexität bewusst und gezielt reduzieren, können daher ein geeignetes Werkzeug sein, um zu verstehen wie Organismen interagieren. So können wir vielleicht eines Tages die Funktionsweise und Stabilität von echten Ökosystemen verstehen.

7. Appendix

7.1. Curriculum vitae

Personalities

Name:	Gregor Kalinkat
Address:	Soderstraße 119, Darmstadt
Date of Birth:	06/28/1977 in Leipzig, Germany

Education

1988-1997:	Grammar school: Wirtemberg-Gymnasium (Stuttgart);
1997:	Abitur (University entrance diploma);
1999-2008:	Biological Sciences, Technische Universität Darmstadt;
2003-2004:	Biological Sciences, Universidad de Alcalá de Henares, Spain; (ERASMUS-scholarship)
2008:	Diploma Degree in Biological sciences;
2008-2012:	Doctoral-Thesis in animal ecology on the topic “Towards an understanding of complexity: How body sizes, preferences and habitat structure constrain predator-prey interactions” at the Technische Universität Darmstadt and Georg-August Universität Göttingen;

Teaching

April-July 2011:	Undergraduate terrestrial ecology field course on plant-insect interaction networks; Teaching appointment (Lehrauftrag), Technische Universität Darmstadt, Faculty of Biology;

Membership

since 2010:	British Ecological Society

Reviewer for the journal

Zoology

7.2. List of publications and talks

a) Articles

Peer reviewed articles

Kalinkat, G., Brose, U., & Rall, B.C. (*in press*): Habitat structure alters top-down control in litter communities. *Oecologia*. doi: 10.1007/s00442-012-2530-6

Rall, B.C., Brose, U., Hartvig, M., **Kalinkat, G.,** Schwarzmüller, F., Vucic-Pestic, O. & Petchey O.L. (2012): Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society B* 367:2923-2934. doi: 10.1098/rstb.2012.0242

Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U. (2011): The allometry of prey preferences. *PLoS ONE* 6(10): e25937. doi: 10.1371/journal.pone.0025937

Rall, B.C., **Kalinkat, G.**, Ott, D., Vucic-Pestic, O. & Brose, U. (2011): Taxonomic versus allometric constraints on non-linear interaction strengths. *Oikos* 120:483-492. doi: 10.1111/j.1600-0706.2010.18860.x – B.C. Rall and G. Kalinkat contributed equally to this study.

Vucic-Pestic, O., Rall, B.C., **Kalinkat, G.** & Brose, U. (2010): Allometric functional response models: body masses constrain interaction strengths. *Journal of Animal Ecology*, 79, 249-256. doi: 10.1111/j.1365-2656.2009.01622.x

Manuscripts in preparation

Kalinkat, G., Schneider, F.D., Guill, C., Digel, C., Brose, U. & Rall, B.C.: Generalised allometric functional responses facilitate predator-prey stability. *manuscript in preparation*

Kalinkat, G., Jacob, U., Rall B.C., & Brose, U.: Body-size signatures in stomach-content based functional responses of Baltic Sea fish species *manuscript in preparation*

b) Posters and talks

Kalinkat, G., Jacob, U., Rall B.C., & Brose, U. (2010): Body-size signatures in stomach-content based functional responses of Baltic Sea fish species - Oral presentation at the British Ecological Society Annual Meeting, Leeds University

Kalinkat, G., Rall, B.C., & Brose, U. (2010): Allometric functional responses constrain consumption preferences of epigeic arthropod predators – Oral presentation at the Gesellschaft für Ökologie Annual Meeting, Giessen University

Kalinkat, G., Rall, B.C., Vucic-Pestic, O., Ott, D. & Brose U (2010): Taxonomic versus allometric constraints on non-linear interaction strengths – Poster presentation at the 3rd Workshop of the ESF Research Network SIZEMIC, Institute of Marine Sciences, Barcelona

Kalinkat, G., Vucic-Pestic, O., Rall, B.C. & Brose, U. (2008): Multi-prey functional responses of arthropod predators and prey body masses – Oral presentation at the British Ecological Society Annual Meeting, Imperial College London

c) Thesis

Kalinkat, G. (2007): Consumption preferences of epigeic spiders driven by prey body mass – Diploma Thesis, Technische Universität Darmstadt

7.3. Ehrenwörtliche Erklärung

Ich erkläre hiermit ehrenwörtlich, dass ich die vorliegende Arbeit selbständig angefertigt habe. Sämtliche aus fremden Quellen direkt oder indirekt übernommene Gedanken sind als solche kenntlich gemacht. Die Arbeit wurde bisher keiner anderen Prüfungsbehörde vorgelegt und noch nicht veröffentlicht.

Darmstadt, den 25. Mai 2012

Gregor Kalinkat

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